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EFFECT OF TEMPERATURE ON THE DEVELOPMENT OF THE EGGS OF A CONCHOSTRACAN PHYLLOPOD, *CAENESTHERIELLA GYNECIA*

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INTRODUCTION

This paper is concerned with studies on the effect of temperature on the development of the eggs of a conchostracan phyllopod, *Caenestheriella gynecia,* which was named and described by one of the writers (Mattox, '49).

The writers express their appreciation for the use of the facilities of the Department of Zoology, at Miami University, Oxford, Ohio, where these studies were completed.

REVIEW OF THE LITERATURE

In reviewing the literature it has been discovered that a controversy existed concerning the development of conchostracan and related phyllopods. The typical life history of conchostracan phyllopods begins with the egg stage. The egg eventually develops into a nauplius, and this stage in turn develops into the adult. Many workers once believed that both drying and freezing of the eggs were necessary for them to develop, while others found that only drying or freezing was necessary, and some workers found that neither was necessary for the eggs of these phyllopods to develop.

Hay and Hay ('89) in contributing to the knowledge of the genus *Branchipus* (*Eubranchipus*) did not specify much beyond the fact that they observed that both drying and freezing were necessary for the young to develop. These workers also mentioned the idea that the winter rains along with a resting period of six months for the eggs which had sunk down into the mud were important factors for their development.

Weaver ('43) did not find that a resting period of six months was necessary, nor did he find that a drying period of a half year or longer was necessary for the eggs of *Eubranchipus vernalis* to develop. Weaver did find, however, that drying of eggs, freezing of eggs, and a long resting period were all conditions occurring in nature. In his experimental work, Weaver found that the eggs of this species hatched in the laboratory after drying without freezing, freezing without drying, as well as after drying and freezing. Dexter ('46) in reporting on further studies on the life history and distribution of *E. vernalis* indicated that he was not successful in hatching a limited number of eggs of this species that were (1) dried, (2) frozen, (3) not subjected to drying or freezing. Dexter and Ferguson ('43) reported that they failed to get the dried eggs of *Eubranchipus serratus* to develop. In another study, on suspended animation, Dexter ('46a) stated

that the eggs of fairy shrimps would usually develop after having been dried.

Shelford ('13) stated that *Eubranchipus* (species not stated) have been found in grassy ponds, and that these ponds do not become completely dry in the summer. In the same report, Shelford reported the case wherein fairy shrimps developed in early winter in Chicago, and died when the cold weather had set in again. In Michigan, Creaser ('29) found species of the same genus in woodland pools, but he did not give any data concerning developmental effects. In 1931, however, Creaser stated that drying might be necessary in some cases but not in all.

Castle ('38) showed that the eggs of *E. vernalis* hatched in an aquarium where freezing and drying of the eggs were not possible. Avery ('39) was successful in hatching eggs of *E. vernalis* which were in a moist condition, while eggs which had been dried failed to hatch.

It has been reported by Ferguson ('35a) that some of the eggs of *Eubranchipus bundyi* hatch the same day that the thin ice at the edge of the pools begins to melt. Ferguson also mentioned the fact that desiccation of the eggs is necessary in some of the North American species. In describing species of *Eubranchipus* new to Canada, Ferguson ('35b) stated that the eggs of *Eubranchipus oregonus* hatched in the fall after the rains had filled the temporary ponds.

In his study of the ecology and zoogeography of the Indian Anostraca, Bond ('34) found that some of the eggs of *Branchipodopsis affinis* required freezing, and that the eggs of *Branchipus* and *Streptocephalus* required drying for development. Without supporting evidence, Bond suggested that it appeared probable that temperature was a very important factor, not only in freezing but also in the maximum ranges for many, if not all, species.

Mathias ('29a) reported that the eggs of *Branchipus schafferi* and *Estheria cycladoides* can be dried and held for some months, and when moistened development and hatching will take place. In continuing with his work Mathias ('29b) in subjecting the eggs to heat found that the eggs of phyllopoda (*Branchipus stagnalis* and *Triops cancriformis*) contained in the earth withstood 80° for one and one-quarter hours without any effect on subsequent development, but when he heated the eggs in contact with water, the eggs in the samples withstood 42° for two and one-quarter hours. In these experiments Mathias found that the nauplii were about one-third smaller than those which had emerged from eggs which were not heated or those which were not subjected to dry heat. Mathias ('29b) also found that a temperature of 80° was the maximum temperature that phyllopod eggs could withstand.

Mathias ('26) who worked on *Chirocephalus* reported that drying was not necessary. He observed that the eggs of this species hatched in sixteen and seventeen days at 15° C., and in thirteen to fourteen days at 18° C. In 1929, Meiklejohn also found that drying is not necessary for the eggs of *Chirocephalus* to develop.

Johansen ('21) found that the eggs of *Branchinecta paludosa* did not hatch until June due to the late thawing of Arctic ice.

Bond ('34) stated he found some *Artemia* eggs that required drying to hatch, and some that required freezing to hatch. No investigation was made to learn if any of the species of phyllopods found in the Yale North India Expedition required both, or whether drying could substitute for freezing or vice versa in any species.

In his discussion on the phyllopods of southeastern Oregon, Coopey ('46) stated that spring thawing served as a stimulus for the eggs of the fairy shrimp to develop.

Gaschott ('28), who worked on material that was quite similar to that of Mathias ('26, '29a, '29b), found that *Triops cancriformis* withstood temperatures from 0° C. to those between 41 and 43° C. with an optimal temperature of 12–25° C.

Packard ('75) in writing on the life-histories of the Crustacea stated that the young of *Limnadia* (*Eulimnadia*) *agassizii* hatched in from five to ten days after the expulsion of the eggs from under the carapace. Cannon ('24) in his work on the development of an estherid crustacean reported that the eggs would only develop if they had dried up in the mud. Berry ('26) reported and described a new species of *Eulimnadia* from Connecticut that completed its life cycle from egg to egg in twenty-three days at temperatures above 33° C. in nature. The eggs were reported to have developed in four to five days, and no information beyond this was given. Mattox ('37) found that *Eulimnadia diversa* completed its life history in fourteen days during the warm summer months.

Gravier and Mathias ('32) reported that the eggs of *Cyzicus cycladoides* (Joly) may be dried, but were observed to hatch without drying in four and one-half days between 12° and 15° C.

One of the writers (Mattox) in 1939 obtained hatching of the eggs of *Cyzicus* (= *Caenestheriella*) which had been (1) dried, (2) kept moist, (3) frozen, and (4) not frozen. These all hatched within a period of three to five days while a second brood of nauplii hatched from three to eight days after the first hatching of the eggs. Mattox ('46), in describing the influence of temperature on the hatching of the eggs of this conchostracan phyllopod, reported success in developing eggs of this genus between 10° C. to 38° C. Mattox also reported that eggs in the dry state exposed to 40° C. would hatch at lower temperatures when placed in water, while eggs exposed to temperatures above 38° C. while in water, failed to hatch when the temperature was lowered. In describing this new species, *Caenestheriella gynecia,* Mattox ('50) stated that hatching of the eggs of this conchostracan phyllopod would occur both in nature and in the laboratory after the watery environment had reached a temperature above 10° C.

Natural Occurrence and Observations of *Caenestheriella gynecia*

In July of 1939 a number of specimens of this conchostracan phyllopod were collected and later named *Caenestheriella gynecia,* sp. nov., Mattox ('50). This phyllopod was collected from a small pool, 11 by 4.2 feet, in a depression, not more than nine inches at its greatest depth, formed by wagon tracks on the outskirts of Oxford, Ohio. This pool is surrounded by black willow (*Salix nigra*), slippery elm (*Ulmus rubra*), Ohio buckeye (*Aesculus glabra*), hackberry (*Celtis occidentalis*).

This temporary pool, which is wholly dependent upon rainfall, was studied by the writers for the above named entomostracan from February 10, 1949 to June 30, 1949. A systematic series of data concerning the habitat and natural occurrence of this conchostracan phyllopod will be found in table I.

From table I it can be seen that the following conditions are encountered in nature for the hatching of the eggs of *C. gynecia* that are probably both dried and frozen before developing into active nauplii: (1) thawing, (2) water, (3) a pond temperature of at least 17° C., (4) air temperature of at least 9.1° C., and (5) a pH range of 6.7 to 7.7.

In addition to the above listed conditions, the following seem to be required for the adults of this entomostracan to thrive successfully: (1) food in the form of various organic substances, and (2) a constant supply of water in the pond so that the adults may have a proper environment in which to develop and drop their eggs while ecdysis is in progress.

The life history of *C. gynecia* includes three stages: (1) egg, (2) nauplius, and (3) adult. All individuals of this species observed have been females, hence the specific name. Eggs for experimental work are easily collected. The egg masses are attached to the exopodite of the 10th swimming appendage in groups of 35 to

TABLE I. *Natural occurrence and observations of* Caenestheriella gynecia

Collection date	Pond temp., ° C.	Air temp., ° C.	pH	Amount of precipitation from previous date, inches	*C. gynecia* observed in habitat	Other animals observed in habitat of *C. gynecia*	Rearing temp., ° C.	Hatching time, hours
Feb. 10, 1949[1]	0	0	—	0.25	None	None	21	48
Feb. 17, 1949	6	5.1	—	1.65	None	None	24.6	49
Feb. 24, 1949	5.7	5.4	—	0.65	None	None	24	49
March 3, 1949	5	3.9	—	0.22	None	None	24.6	69
March 10, 1949	4.7	3.9	—	3.15	None	None	25	72
March 17, 1949	4.4	1.7	—	0.00	None	None	22	44
March 24, 1949	10.5	5.6	6.8	0.00	None	R, F, G, T.	22	41
April 3, 1949	12	6.9	6.8	0.51	None	R, F, G, T, A.	20	37
April 10, 1949	12	6.1	6.8	0.17	None	R, F, G, A.	21	30
April 17, 1949[2]	17	9.1	6.8	0.52	Nauplii	R, G, C, F, A.	Nauplii collected in nature; above procedure not necessary.	
April 24, 1949	17	13.9	6.8	0.00	Nauplii	R, G, C, F, A.		
April 26, 1949	21	16.7	7.7	0.00	Many naupl.	R, G, C, F, A, Co.		
April 28, 1949	17	12.2	7.7	0.00	Many naupl.	R, G, C, F, A, Co.		
May 3, 1949	22	19.4	6.7	0.35	Many naupl.	R, G, C, F, A, Co.		
May 10, 1949	20	17.8	6.7	0.00	Many naupl.	O, F, A, C, Co.		
May 13, 1949	18	17.8	7.7	0.00	Naupl. and Ad.	O, F, A, C, Co.		
May 20, 1949	17	11.7	7.7	0.35	Naupl. and Ad.	O, F, A.		
May 26, 1949	18	16.7	7.5	1.11	Naupl. and Ad.	O, F, A.		
May 31, 1949	17	15.6	6.7	0.00	Naupl.; Ad. E.	O, F, A.		
June 4, 1949	21	10.3	6.7	0.00	Naupl.; Ad. E.	O, F, A.; Cu. lar.		
June 7, 1949	19	15.6	6.8	0.00	Naupl.; Ad. E.	O, F, A.; Cu. lar.		
June 13, 1949	20.5	24	7.7	1.65	Naupl.; Ad. E.	O, F, A.; Cu. lar.		
June 16, 1949	20	22	6.7	2.64	Naupl.; Ad. E.	O, F, A.; Cu. lar.		
June 20, 1949	24	22	6.7	0.25	Naupl.; Ad. E.	O, F, A.; Cu. lar.		
June 25, 1949	24	26	6.7	0.65	Naupl.; Ad. E.	O, F, A.; Cu. lar.		
June 28, 1949	22.5	25	6.7	1.45	Naupl.; Ad. E.	O, F, A.; Cu. lar.		
June 30, 1949	27	29	7.7	0.00	Naupl.; Ad. E.	O, F, A.; Cu. lar.		

[1] From Feb. 10 to April 10 mud containing eggs of *C. gynecia* was collected.
[2] From April 17 to June 30 nauplii, adults, and/or adults with eggs of this species were collected.
Abbreviations: A., Amoebas; Ad., Adults; Ad.E., Adults carrying eggs; C., Cladocera; Co., Copepods; Cu. lar., Culicidae larvae; F., Flagellates; G., Gastrotrichs; Naupl., Nauplii; O., Ostracods; R., Rotifers; T., Tardigrads.

120. During ecdysis these masses are thus cast off and easily collected with the molted skeleton.

Under experimentally controlled conditions, it was found that the complete life history of *C. gynecia* from egg to the stage where the adult is carrying eggs requires twenty-three days.

LABORATORY METHODS

Prior to the experimental work involved in this problem, mud was obtained from natural sources so that adults could be reared in the laboratory and watched for eggs. Mud was collected at least once every week from the pool where adults had been previously collected. Since this phyllopod was observed from July, 1939, it was presumed that the collected mud would contain eggs that had been dried and frozen from the previous year.

In an effort to duplicate conditions found in nature that would produce nauplii, portions of the collected mud were (1) thoroughly dried in a temperature range of 35° C. to 56° C., (2) frozen at 0° C., (3) set at temperatures from 0° C. to 78° C., (4) quickly dried, (5) quickly frozen. Water was placed in the dried, frozen, and wet portions. All of these were carefully observed at each temperature for the first appearance of nauplii. After the nauplii were obtained, many were reared to the adult stage and carefully observed for eggs. These eggs, in turn, were used during this work.

The eggs for this experimental work were obtained from two chief sources: (1) from full grown adults hatched in

the laboratory, and (2) from adults obtained in nature. The latter were reared in the laboratory and observed many times during the day for eggs. In an effort to get the eggs without too much difficulty, two to three adults were placed in small stender dishes with water. Immediately after ecdysis the eggs were collected and stored in small vials at room temperature. The method proved very successful, and a good supply of at least 1,000 to 1,500 eggs remained ready for use daily.

After the eggs were obtained, they were put to experimental use promptly, or as soon as possible. Some of the eggs were frozen, while others were dried, dried and frozen, kept at room temperature, and finally subjected in numbers of 20 to 35 to a series of temperatures in water. The latter was attempted in an effort to ascertain (1) the optimum temperature required for the development of eggs, (2) the maximum temperature, (3) the minimum temperature.

Five electrical devices were used for the development of the eggs. First, a constant temperature water bath was constructed and utilized for temperature increments of 1° C. from 11° C. to 45° C.; secondly, a temperature range of 0° C. to 10° C. was obtained by placing eggs at various distances from the freezing compartment in a General Motors Frigidaire; thirdly, an incubator was used for a temperature range of 33° C. to 38° C., and lastly, a paraffin bath oven and a copper oven were used for temperatures up to 80° C.

Two sets of eggs, (1) wet and (2) dried, were used throughout the entire study. The wet eggs were not exposed to any form of desiccation, but were maintained in airtight vials until used. In

TABLE II.—*Effect of temperature on the development of the eggs of* Caenestheriella gynecia

Wet ova			Dry ova		
Temperature of ova, ° C.	Temperature of water, ° C.	Hatching time	Temperature of ova, ° C.	Temperature of water, ° C.	Hatching time
0–12	0–12	—	0–12	0–12	—
13	13	21 days	13	13	—
14	14	17.9 days	14	14	—
15	15	16.5 days	15	15	—
16	16	15 days	16	16	—
17	17	13.9 days	17	17	18 days
18	18	13.05 days	18	18	16.05 days
19	19	11 days	19	19	15 days
20	20	9.05 days	20	20	13 days
21	21	7.05 days	21	21	12 days
22	22	6.05 days	22	22	10 days
23	23	4.5 days	23	23	7.9 days
24	24	2.7 days	24	24	5 days
24–25	25	2.1 days	24–25	25	3.7 days
24–26	26	44 hours	24–26	26	2.4 days
24–27	27	39.25 hours	24–27	27	2 days
24–28	28	32 hours	24–28	28	35 hours
24–29	29	34 hours	24–29	29	38 hours
24–30	30	38.25 hours	24–30	30	41 hours
24–31	31	42.50 hours	24–31	31	46 hours
24–32	32	46 hours	24–32	32	2.3 days
24–33	33	48 hours	24–33	33	2.4 days
24–34	34	2.2 days	24–34	34	2.5 days
24–35	35	2.3 days	24–35	35	4 days
24–36	36	2.5 days	24–36	36	5.05 days
24–37	37	3 days	24–37	37	6.4 days
24–38	38	3.8 days	23–38	38	7.7 days
24–39	39	—	24–39	39	—
24–40	40	—	24–40	40	—

some temperature ranges, the eggs were both frozen and dried to see what effect this would have on their development. Since the results showed that both drying and freezing were not required for development, the latter was not pursued too extensively. The series of dry eggs were dried for varying lengths of time, the period of desiccation seemed not to be too important so far as hatching time is concerned.

Observations stopped with the hatching of the nauplius stage.

Experimental Data

In table II the data obtained in the experimental work will be found.

The items "temperature of ova," "temperature of water," and "hatching time" in the table are interpreted as follows: (1) "temperature of ova" indicated the temperature at which the ova were maintained, for varying periods of time, prior to the time they were put to experimental use; (2) "temperature of water" indicated the temperature of the water in which the eggs were placed for development and hatching; and (3) "hatching time" is a record of the average time it took for the eggs to hatch.

In examining table II, it will be seen that the eggs, both wet and dry, of *C. gynecia* do not show any noticeable signs of development in a temperature range of 0° C. to 12° C. in a period of thirty days. The eggs in this and all other series were

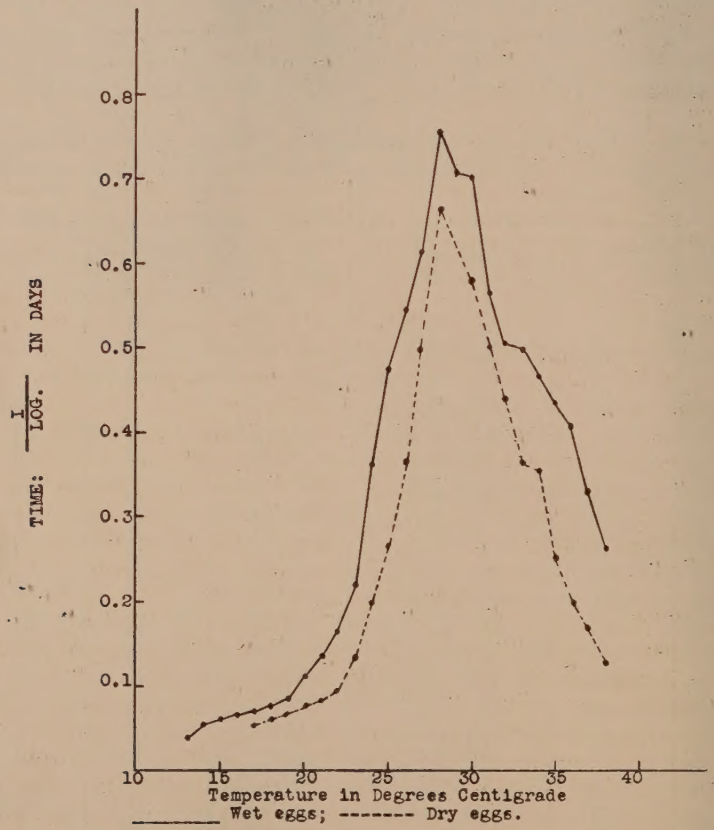

Fig. 1. Correlation of temperature and time required for the wet and dry eggs of *C. gynecia* to hatch.

carefully examined to see if any water had been imbibed, an important process in the development of these eggs (Mattox, '50).

The first development for the wet eggs of *C. gynecia* requires twenty-one days at 13° C. This is the minimum temperature required for complete hatching into a free swimming nauplius with two pairs of appendages, the second antennae and mandibles. In the Anostraca and Notostraca, however, the larvae are typical metanauplii at the time of hatching, and appear as regular crustacean larvae. The results shown in table II are interesting for many reasons. The dried eggs hatched for the first time at 17° C., the temperature at which nauplii were first observed in nature. It can also be seen that a gradual decline in the number of days required for hatching of both wet and dried eggs was encountered when the temperature was increased in intervals of 1° C. up to 28° C. This can best be observed by examining figure 1 which shows correlations of temperature with time required for development. Up to 28° C. it can readily be seen that drying tends to retard the time required for development. At 29° C., however, it will be observed for the first time that increase of one degree centigrade tends to retard development in both the wet and dried eggs. Figure 1 shows a definite change in the direction of the curve at this temperature, and table II indicates consistently that a rise of one degree centigrade, above 28° C., retards development.

Pearse ('26) states that *Artemia* eggs do not hatch sooner at higher temperatures. Pearse does not mention anything beyond the statement above, but there is strong evidence that he is correct since the same has been encountered in this series of experiments.

Since temperature definitely affects the development of these eggs, the writers are of the opinion that the physiology of the eggs has a great deal to do with the way in which they develop. This may account for the differences in the rate of development. A study of the physiology of the eggs of *C. gynecia* was not attempted at this time since this report was restricted to temperature effects.

From table I it can readily be seen that 38° C. is the maximum temperature for development of both the wet and dried eggs. At 39° C. heat rigor was observed in the wet series, and no development whatsoever was observed in the dry series. After five days at 40° C., the wet eggs showed definite signs of heat rigor.

Discussion

These experiments were directly concerned with the effect of temperature on the development of the eggs of a conchostracan phyllopod, *Caenestheriella gynecia,* and the results have bearing on the controversy concerning the effect of temperature on the eggs of phyllopods in general.

Throughout the experiments, there were many indications that the temperature effects on *C. gynecia,* such as maximum temperature effects, size of nauplii at different temperatures, and the overall effect of temperature on their development, were similar to those on anostracan and notostracan phyllopods. In some respects, however, the conchostracan was found to differ.

The results given in table II do not show any definite signs of resemblance to the conditions of anostracan phyllopods. Many workers have reported hatching of the dried eggs of *Eubranchipus* immediately after thawing. Gaschott ('28) indicated that *Triops cancriformis,* a notostracan, could develop at 0° C., and that it could withstand a temperature range of 0° to 41° C. Gaschott ('28) reported that *Tanymastix stagnalis* developed in a range of 8° to 22° C. This notostracan not only develops sooner than *Triops,* but it also develops sooner than the anostracan and conchostracan phyllopods.

In addition to the experimental results reported in table II, several experiments were performed in an effort to ascertain the time required for the eggs that were

both dried and frozen in nature to develop. This has been reported partially in table I.

The following was observed from mud that was dried and frozen in nature, mud from which eggs of *C. gynecia* were previously collected.

Temperature at which mud was collected,—° C.	Temperature of water, ° C.	Time required for hatching, hrs.
0	21	60
0	25.5	96
0	27	98
4.4	22	46
5.7	24	49
6	24.6	48
6	25.2	57¼
10.5	22	41
12	20	37
12	21	38

From the above data, it is seen that 37 to 98 hours are required for the eggs that are dried and frozen to develop and hatch in a temperature range of 0° to 27° C. As compared with the optimum temperature range of the wet eggs, 24° to 37° C., which require 32 to 72 hours for hatching, it is apparent that drying and freezing are not necessary for the eggs of *C. gynecia* to develop and hatch into active nauplii.

On June 6, 1941, one of the writers (Mattox) stored some eggs of this phyllopod with water in a light-excluded bottle at room temperature, and on February 15, 1949, the contents were examined. The eggs were present, but no nauplii were found. The entire contents were then set into fresh tap water at 21° C. in a transparent bell-dish with an extremely wide mouth, thus allowing air to move freely throughout the dish. Nauplii appeared after a period of six days, and they were found swimming (jerking) in their characteristic way.

Also, eggs collected during July 1939 were dried in the original mud and kept in the laboratory in a dry state. These eggs were placed in fresh water on August 1, 1944; the water temperature was approximately 24° C. Six days later on August 7, nauplii appeared in large numbers. Further hatching of nauplii occurred daily for 12 days after which no new nauplii were observed.

The upper limit of viability of these eggs is not known. However, as is here indicated the eggs do remain viable in water without hatching for a period of nearly eight years and in a dry state for 5 years.

The optimum temperature range for the wet eggs of *C. gynecia* appears to be 24° to 37° C. while 26° to 34° C. seems to be the optimum range for the dry eggs of this species. The mean optimum temperature for the development of these eggs, as judged from results here reported, seems to be 28° C. In comparison to the optima for this phyllopod, 21° to 24° C. has been reported for *Artemia* (Anon., '47), and ranges of 12° to 25° C. for *Triops* and 8° to 22° C. for *Tanymastix* have been reported by Gaschott ('28).

A complete examination of the data of these experiments and of the results of other workers reported herein will show that this study of the effect of temperature on the development of the eggs of *C. gynecia* is more conclusive since a complete temperature study was made including a series of observations in nature.

Temperature seems to have an effect on the development of the eggs of *C. gynecia* as indicated by: (1) the time required for development and hatching, which varies with each change in temperature, and (2) the size of the hatched nauplius, which is 0.37 mm. in the optimum range, and is approximately nine per cent smaller, in size, above the optimum range.

Summary and Conclusions

1. The writers attempted to learn the effect of temperature on the development of the eggs of *Caenestheriella gynecia.*

2. It is apparent that the temperature in nature as well as in the laboratory has a definite effect upon the development and hatching of the eggs of *C. gynecia.*

3. Field observations indicate that a

minimum air temperature of 9.1° C. and a pond temperature of 17° C. is necessary for the nauplii of this species to appear.

4. The minimum temperature for the hatching of wet and dried eggs of this conchostracan phyllopod seems to be 13° and 17° C., respectively, while 38° C. appears to be the maximum temperature for both wet and dried eggs.

5. The results of these experiments indicate that the optimum range for development of the wet eggs is 24° to 37° C., and 26° to 34° C. for the dry eggs, with a time interval of 32 to 72 hours required for hatching of the wet eggs and 35 to 57 hours for the dried eggs.

6. The Van't Hoff principle does not seem to be followed in these experiments.

7. There seems to be a tendency for heat rigor to set in when the wet eggs of this phyllopod are subjected to a temperature of 39° C. or above.

8. Heat rigor is observed at 40° C. in the wet series.

9. No development or hatching seems to take place above 38° C. in the dry series.

10. The size of the nauplii when hatched decreased approximately nine per cent at temperatures above the optimum.

11. Hatching will take place without drying and freezing as added stimuli.

12. Eggs maintained in water in a dark and hermetically sealed bottle for nearly 8 years hatched when introduced into fresh aerated water.

13. Eggs hatched after remaining in the dry state for a period of 5 years.

14. Drying tends to retard the development and hatching of these eggs.

15. A resting period is not necessary for these eggs to develop.

16. There is some evidence that a study of the physiology of the eggs would add more information to what is known concerning the development of phyllopod eggs.

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VEGETATION ZONES OF MEXICO

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The present classification and map (fig. 1) of Mexican vegetation was compiled as part of a survey of the wildlife resources of Mexico.[1] The objective has been to divide the country into natural biogeographical units, thereby simplifying consideration of the problems of wildlife distribution and wildlife conservation. No attempt is made to critically define the structure of individual plant communities or the ecological affinities of the several communities included in each major zone or type. That is a task for the plant ecologist. The present classification, though crude, is yet accurate enough to satisfy many practical needs. No similar map of equal accuracy and detail is currently available.

Selection of the twelve vegetation types was governed largely by my own observation in the field. But in tracing the distribution of types, full use has been made of the botanical literature and of generous personal advice from three field botanists thoroughly familiar with the Mexican flora—Aaron J. Sharp, Charles L. Gilly and Howard S. Gentry.

I am indebted to Faustino Miranda, formerly of the Instituto de Biología, México, D.F., for identification of the plants collected during the field survey. Plant names derived from the literature are listed as given by the respective authors, save that spelling is made to correspond to Standley's manual ('20–'26) insofar as possible.

Each vegetational type or "formation" is a composite of many recognizably distinct communities, some of which are indicated in the text that follows. I admit to many arbitrary decisions on where to divide adjoining types or in which to include a given community. Also, there are countless areas of intergradation between types which are not shown. Local juxtaposition of types is of great importance to game, as where fingers of mesquite reach across the desert or patches of manzanita occur on dry south exposures within the pine-oak uplands. These conditions must be understood but they cannot be indicated on a small scale map.

Nor are the changes in vegetation resulting from human occupation shown. The Valley of Mexico is designated as "pine-oak forest" although it is now stripped of its trees (so also are the hills around Zacatecas, Pachuca, Taxco and several hundred other cities). The tropical forests of Yucatan have been almost entirely reduced to second-growth scrub by the age-old Mayan system of rotating milpas (corn fields). These secondary changes in the landscape are not considered here. The map is meant to show original climax vegetational types.

Certain well-defined types of unquestioned ecological significance are not recognized because their distribution is too limited to map at small scale. The following examples might be mentioned:

1. Arctic-Alpine meadows on the crests of major volcanoes.
2. The xeric vegetation of lava flows (under edaphic rather than climatic control).
3. Littoral communities such as salt marsh, mangrove swamp and dune grassland.
4. Aquatic communities.

The mangrove swamps in particular are of importance as game habitat, and it is worth inserting parenthetically that mangroves extend up the Gulf coast to southern Tamaulipas and up the Pacific coast to Tiburón Island, Sonora, and Santa Rosalía, Baja California.

[1] Survey supported by Pan American Union and Comisión Impulsora y Coordinadora de la Investigación Científica, México, D. F.

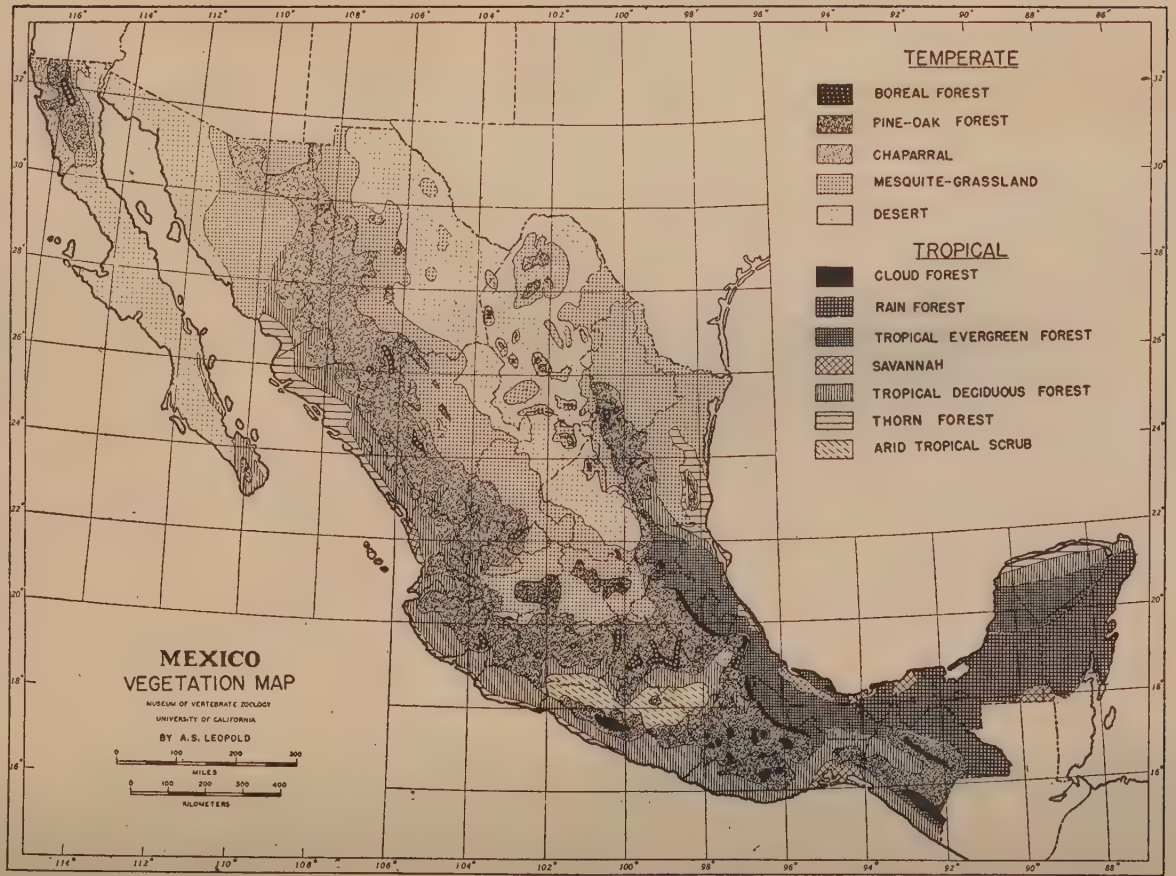

FIG. 1. Map of the vegetation zones of Mexico, prepared from original observations by the writer and from literature cited at the end of the paper.

TABLE I. *Approximate areas included in, and rainfall data pertaining to the vegetation zones*

Zone	Per cent of total land area	Approximate area in square miles	Range of annual rainfall in inches*
Temperate			
Boreal forest	.5	3,800	30–74
Pine-oak forest	25.8	195,600	18–70
Chaparral	1.2	9,100	14–30
Mesquite-grassland	21.6	163,700	9–36
Desert	23.1	175,100	2–15
Tropical			
Cloud forest	.5	3,800	70–200
Rain forest	7.3	55,300	60–200
Tropical evergreen forest	5.5	41,700	36–112
Savannah	.9	6,800	34–100
Tropical deciduous forest	9.1	69,000	24–60
Thorn forest	3.2	24,300	16–34
Arid tropical scrub	1.3	9,800	12–28
	100.0	758,000	

*From data presented by Contreras Arias (1942).

The accompanying table (table I) lists the twelve vegetation types and the area in Mexico occupied by each. Areas were ascertained by planimeter from the map.

The temperate and tropical series are each arranged roughly in order of decreasing humidity. On the whole, the frost line can be said to divide the two series, but this concept cannot be adhered to rigidly. In southern Tamaulipas, for example, where the temperate and tropical regions meet, there occurs an overlapping of the arid types in each series with the result that temperate mesquite-grassland occupies a hot inland basin (valley of the Río Guayalejo), surrounded by tropical deciduous forest and thorn forest on the cooler and more humid foothills. In southern Sonora the tropical deciduous forest reaches far up the Río Yaqui valley, but the Yaqui delta is temperate mesquite-grassland. Cloud forest and pine-oak forest often intermingle. In short, exact lines of demarcation between the temperate and tropical types are not always as evident in the field as the map might imply.

TEMPERATE VEGETATION TYPES

Boreal forest

The Boreal zone in Mexico is confined to the high volcanic peaks that range across the country between the 18th and 20th parallels and to a few scattered peaks in the northern cordilleras (Sierra Madre Oriental and Sierra Madre Occidental). Included in this zone, under the loose term "Boreal Forest," are all associations above the Transition Zone of Merriam (1898)—principally Canadian and Hudsonian Zone forests. A few alpine meadows exist on the tops of the highest volcanoes but the areas are too small to warrant separate treatment here.

Leavenworth ('46) offers the following excellent analysis of the various boreal communities on Mt. Tancítaro, Michoacán. The flora of nearby Mt. Angahuán is similarly analyzed by Eggler ('48).

a. Open pine and bunchgrass.—This occurs at 9,500 to 11,800 feet (crest). The pine is the stunted *Pinus montezumae* var. *rudis.* Scattered junipers (*Juniperus tetragona*) and the ericaceous shrub *Pernettia ciliata* form a low mat in places, but the understory is dominated by coarse grasses of the genera *Festuca, Muhlenbergia,* and *Agrostis.*

b. Fir forest—This occurs at 7,500 to 9,500 feet in heads of canyons. In places the fir *Abies religiosa* forms almost pure stands with only mosses and lichens surviving beneath the dense canopy. This is the belt of heaviest fog (Eggler '48).

c. Pine-alder-fir.—This occurs from 7,200 to 8,500 feet, mostly in lower stream valleys. The two principal pines are *Pinus montezumae* and *P. ayacahuite,* and the fir *Abies religiosa.* Leavenworth calls the alder *Alnus glabrata,* which perhaps is the same species as that listed by Eggler as *A. jorullensis.* Traces of "Cloud Forest" exist in the deep canyons well up on Mt. Tancítaro.

This classification of boreal communities applies fairly well throughout the volcanic zone farther east along the 19th parallel. At Tres Marías, Morelos, between 9,500 and 10,500 feet, the pine-bunchgrass community, with *Pinus montezumae* and *Festuca tolucensis* as dominants, covers large areas; *Alnus firmifolia* and the shrub *Senecio cinerari-*

oides form thickets in the hollows and on cool north slopes. At Mil Cumbres, Michoacán, and on the uplands surrounding the Toluca Valley, Estado de México, fir (*Abies religiosa*) is dominant in the forests up to 10,500 feet.

The exact altitudinal range occupied by each plant community varies with slope, latitude, exposure, and nearness of other peaks or ridges, but the order of occurrence (vertical arrangement of communities) is generally constant on all the high peaks of southern Mexico.

Muller ('39) describes the boreal forest on Cerro de Potosí, the highest mountain in the Sierra Madre Oriental of Nuevo León. Above 8,500 feet the forest is dominated by *Pinus montezumae,* with *P. ayacahuite* and *Pseudotsuga mucronata* attaining equal importance on moist sites. Near the crest *P. montezumae* in the stunted alpine form (var. *Hartwegii*) remains the dominant tree, with *P. flexilis* and *Juniperus mexicana* occurring in recumbent shrubby mats at timberline. A small alpine meadow covers the crest itself, which, according to Muller, is 3,800 meters or 12,460 feet above sea level.

I have less exact information on the occurrence of a boreal flora in northwestern Mexico. Nelson and Goldman ('26: 586) state that the "Fir-spruce Association [Canadian and Hudsonian zones] . . . includes very limited areas on the extreme upper slopes of the San Pedro Mártir Mountains in northern Lower California, [and] a few peaks along the crest of the Sierra Madre Occidental. . . ." Elsewhere Nelson ('21) enumerates the boreal species occurring on the San Pedro Mártir, including *Abies concolor, Pinus contorta, Populus tremuloides* and *Symphoricarpos parishii,* all of which are well-known components of the Canadian Zone in southern California.

Merriam (1898) mapped the boreal zone as almost a continuous band following the crest of the Sierra Madre Occidental, which is hardly the case. At Los Flores, 25 km south of Durango City, Durango, I found Douglas fir (*Pseudotsuga*) dominant in north-facing canyons at 7,500 feet but absent on level mesas. The principal pine is the ubiquitous *P. montezumae.* On the divide west of Colonia Pacheco, Chihuahua, *Pseudotsuga* was nowhere in evidence at 7,000 feet. In preparing the map I have designated only a few of the highest peaks in Chihuahua and Durango as boreal, and this is provisional since no floristic analyses of these peaks seem to be available.

Pine-oak forest

From the standpoint of game, and likewise of human economics, the pine-oak zone is the most important vegetational type in Mexico. It is also the largest. Many distinct communities are included, from oak scrub bordering the northern deserts to high pine forests intermingling with the lower fringe of the firs. Standley ('20–'26) lists 112 species of oaks in Mexico and all of these appear somewhere within the zone. Likewise, of the 39 Mexican pines enumerated by Martinez ('45), all except a few boreal species occur here. Because of the great number of species involved and the numerous combinations in which they occur, I cannot offer a complete list of the communities comprising the pine-oak zone. All, however, fall into the following four general types, of which examples are given.

a. Pine forest.—Dense forests within the pine-oak zone are usually made up largely of pines, oaks being subdominant or sometimes absent. In central and southern Mexico, the commonest pine and the one most generally occurring in tall dense stands is *Pinus montezumae.* This species is important as far north as Durango in the western mountains (Brand '36) and Nuevo León in the east (Muller '39). In the great pinelands of Chihuahua, Shreve ('39) lists *Pinus apacheca, P. chihuahuana, P. arizonica, P. lumholtzii* and *P. ayacahuite.* At Omiltéme, Guerrero, in the Sierra Madre del Sur, I found the dominant pines to be *P. her-*

rerai on ridges and north slopes and *P. pseudostrobus* on south slopes.

Often the high pine forests blend into the boreal zone in such a manner that drawing a dividing line is purely arbitrary. This is illustrated by the distribution of *P. montezumae* which is an important component of both zones in the southern uplands.

b. Pine-oak woodland.—Open, scattered stands may be dominated by pines in some places, by oaks in others. Usually these woodlands occur between the oak scrub and high pine forest, but there are exceptions to this arrangement. On the Sierra de Tamaulipas an oak woodland covers the high mesas and ridges, adjoined immediately below by tropical deciduous forest. There is no oak scrub belt. The dominant oak in this case is *Quercus arizonica.* In Nuevo León, Muller ('39) lists the following species as occurring between the lower oak scrub and the high pine forests: *Pinus montezumae, P. pseudostrobus, P. teocote, Quercus greggii* and *Q. mexicana.* In places these grow in open woodland stands. The upper oak belt in Chihuahua, between oak scrub and pine forest, is dominated by *Quercus hypoleuca, Q. pennivenia, Q. sipuraca* and *Q. epileuca* (Shreve '39). Scattered pines occur in these stands but oaks are more numerous. Below Omiltéme, Guerrero, the oak woodland is comprised of *Q. acutifolia, Q. lanigera* and *Q. candicans.*

c. Piñon-juniper woodland.—Martinez ('45) classifies the Mexican piñons as follows: *Pinus cembroides, P. cembroides* var. *edulis, P. pinceana* and *P. nelsoni,* found on the northern and central Mexican plateau; and *P. monophylla* and *P. quadrifolia* found in northern Baja California. These species normally occur in scattered woodland stands on arid foothills or low desert ranges. They may be mixed with junipers or more rarely with scrub oaks or elements of chaparral (manzanita, etc.).

d. Oak scrub.—This usually occurs along the lower fringes of the pine-oak zone adjoining semi-arid foothills or lowland basins. Around the base of the mountains in Nuevo León, Muller ('39) lists the following dominant species: *Quercus clavicola, Q. canbyi, Q. porphyrogenita* and *Q. fusiformis.* In central Puebla the oak belt ("encinar") bordering the tropical valley of the Río Balsas is dominated by *Q. glaucophylla* and *Q. glaucoides* (Miranda '42). Along the eastern fringe of the Chihuahua mountains bordering the short grass, common oaks are *Q. santaclarensis, Q. grisea* and *Q. emoryi* (Leseur '45, Brand '36). Locally these oaks extend far into the foothill zone shown on the map as mesquite-grassland.

The Indian population of Mexico always has centered on the southern uplands, from Jalisco through Michoacán, Edo. de México, Puebla and Oaxaca to Chiapas. Some tribes, most notably the Mayans and their relatives, have colonized the low tropics, but they are a minority. From early times to the present, the greatest part of the Mexican population has lived in the pine-oak zone with its healthy, temperate climate suitable for the cultivation of corn. As a result of this concentration the forests, soils, wildlife and other natural resources of the southern uplands have been severely taxed and in some localities largely destroyed, while great areas of the tropics remain virtually untouched. The conservation problem in Mexico centers around the uneven distribution of people and the undue demands made on the pine-oak uplands.

Chaparral

Typical California chaparral extends approximately two hundred miles down the outer coast of Baja California, between the mountains and the Pacific. Following Nelson ('21), I have mapped the chaparral as extending only to the 30th parallel. In the coastal fog belt below that point the brush gives way gradually to desert vegetation which para-

doxically is laden with epiphytic mosses and lichens.

California chaparral is a well-known vegetational formation comprised of such genera as *Adenostoma, Rhus, Ceanothus, Quercus, Artemisia, Prunus, Eriogonum, Arctostaphylos* and *Cercocarpus.*

Some localities in northeastern Mexico support a vegetation closely related to California chaparral. Along the western base of the Sierra Madre Oriental in Nuevo León, Muller ('39) describes a brush type composed of *Rhus, Ceanothus, Quercus, Cercocarpus, Samuela* (*Yucca*), *Arbutus* and *Arctostaphylos.* Elsewhere in Coahuila (Shreve '42) and Nuevo León, many of the same genera occur in the scrub oak belt. These localities are not designated as chaparral on the map, however, because of their limited area.

Mesquite-grassland

Included in mesquite-grassland are several well marked plant communities which have in common a ground cover dominated by grasses, usually species of grama (*Bouteloua*). Along the eastern base of the Sierra Madre Occidental and on some high ridges and plateaus in Coahuila the grama grasses form an almost continuous sod with few or no woody plants or succulents present. This community is called "short-grass plain." In northeastern Mexico and locally in Sonora the grama sod is heavily interspersed with shrubs and low trees, the most important form being mesquite (*Prosopis*). I have designated this combination as "mesquite scrub." Transitional between these two types and desert proper may occur a mixed desert-grassland vegetation which Shreve ('42) calls "cactus-acacia-grassland;" this is particularly characteristic of the western margin of the central desert. An ecologically distinct type of grassland, the "Gulf coast bluestem prairie," is thrown into this general group for lack of a better place to include it. The bluestem prairie is an important vegetational formation along the coast of Texas, and it extends into northeastern Tamaulipas in a narrow coastal strip.

a. Short-grass plain.—In Chihuahua, Durango and Zacatecas the dominant grasses are gramas, the commonest species being *Bouteloua gracilis* (Shreve '39, '42, Leseur '45). Gramas likewise are dominant on the eastern border of the desert (Muller '39). Along the edge of the oaks and in fact forming an important component of the oak scrub community are grasses of the following genera: *Bouteloua, Andropogon, Aristida, Eragrostis, Muhlenbergia* and *Oryzopsis.* The great "Bajío" of Guanajuato, Jalisco and Michoacán, a rich basin of deep soil which is now all in highly productive agriculture, probably supported an original vegetation of bunchgrasses.

b. Mesquite scrub.—The most characteristic plant is the mesquite itself, which likewise happens to be an important food and cover plant for game. In southern Sonora, Shreve ('34) lists as dominants of this community *Prosopis velutina, Olneya tesota, Cercidium microphyllum* and *Encelia farinosa. Prosopis* also is an important shrub on the delta of the Colorado River and along waterways throughout the central desert as far south as Hidalgo and central Jalisco. In each of these sites there is usually a ground cover of bunchgrasses, mostly gramas.

In northeastern Mexico, mesquite likewise is a characteristic plant of the arid scrub, but it often shares dominance with shrubs of the genera *Acacia* and *Cordia.* Muller ('39) recognizes the following two communities in northern Nuevo León: "East coastal plain scrub," characterized by *Cordia boissieri, Acacia amentacea, A. wrightii, A. berlandieri, Yucca treculeana* and others including *Prosopis chilense.* He states: "In the northern tip [of Nuevo León] the principal vegetation type is characterized by *Prosopis chilense* and *Opuntia* sp. forming a savannah on *Bouteloua trifida, Aristida purpurea, Triodia pilosa* and *T. texana.*" In the southern and central parts of the coastal plain (of Tamaulipas as

well as Nuevo León) *Acacia* and *Cordia* are of greater importance than mesquite. The second type of scrub listed by Muller is "Piedmont scrub" occurring in the Sierra foothills and on prominent hills on the coastal plain. *Quercus fusiformis, Leucaena glauca, Cordia boissiera* and *Acacia farnesiana* are the principal shrub species.

A small area of mesquite scrub occurs in eastern Puebla in the rain shadow of the volcanoes Orizaba and Perote. In addition to *Prosopis, Celtis, Fouquieria* and *Acacia* there is a heavy growth of cacti and agaves. The escaped pepper tree (*Schinus molle*) likewise is conspicuous.

c. Cactus-acacia-grassland.—This includes the following assemblage of desert and grassland species (Shreve '42): *Acacia tortuosa, Prosopis* sp., *Celtis pallida, Acacia paucispina, Opuntia* (three species), *Yucca carnerosana, Bouteloua* (three species), *Aristida divaricata* and *Eragrostis mexicana.*

d. The Gulf Coast bluestem prairie.—This originally was dominated by tall bunchgrasses of the genus *Andropogon* on well-drained sites, sloughs and depressions being occupied by cordgrass, *Spartina spartinae.* As a result of grazing, much of the *Andropogon* has been heavily invaded by mesquite and scrub oak, with the result that this "grassland" is now largely occupied by brush.

Desert

The great desert areas of northern Mexico support in fact a good deal of vegetation and a surprising amount of game.

a. Cactus desert.—This adjoins the lower edge of the mesquite-grassland and supports a richer biota than other desert communities. Dominant plants may be cacti and yuccas as in eastern San Luis Potosí or assorted shrubs as reported for eastern Durango by Gentry (Ecologic survey of the Durango highlands, unpublished ms.) under the type name "chaparillo": *Cordia greggii, Atriplex* sp., *Koeberlinia spinosa, Buddleia marrubiifolia* and *Euphorbia antisyphilitica.* Subdominant species may be Mariola, Guayule, *Agave lechugilla, Larrea* sp., and along watercourses mesquite and hackberry. Stands of these plants often are quite dense and most desert game occurs in this belt.

b. Creosote bush desert.—This is characterized by open, sparse vegetation generally dominated by a species of *Larrea;* it is often called the "desert-shrub" community. Examples of this type follow: Sonora and Baja California, Shreve ('34)—*Larrea tridentata* and *Franseria dumosa* dominant; *Prosopis velutina, Opuntia ramosissima* and *Acacia greggii* along watercourses.

Chihuahua, Shreve ('39)—*Larrea* and *Flourensia cernua* dominant; in valleys *Prosopis, Acacia, Celtis,* and *Opuntia.*

Western Nuevo León, Muller ('39)—*Larrea divaricata, Dasylirion texanum, Agave falcata* and *Fouquieria splendens;* along watercourses *Prosopis chilense, Celtis pallida, Mimosa biuncifera, Acacia greggii* and *Opuntia imbricata.*

c. Hilaria basins and alkaline flats.—This occurs in closed depressions of the Chihuahua desert that have no outside drainage. The alkaline flats may be seasonally covered with water and support no vegetation whatsoever. Parts of these "llanos" or "bolsones" that are not subject to flooding support almost pure stands of *Hilaria mutica,* a rather wiry, unpalatable grass of little value to wildlife or livestock.

Tropical Vegetation Types

Cloud forest

The cloud forest in Mexico generally is made up of two distinct elements—temperate montane hardwood or pine-oak forest and a tropical undergrowth of low trees, shrubs, herbs, vines and epiphytes. Such combinations occur on temperate peaks or escarpments (usually above 5,000 feet) that are swept by moisture-laden air currents rising from tropical

lowlands. Because the dominant trees are temperate species, the formation might well be included in the Temperate rather than the Tropical vegetation series. It is often called "sub-tropical" or "temperate rain forest" (Beard '44). Even though I well realize that designating cloud forest as tropical is equivocal, I list it here because the biota as a whole is largely of tropical affinities. The character of the forest is determined more by the heavy tropical understory than by the overstory. Also, most of the vertebrates found in cloud forest are of tropical genera. The climate is usually cool and decidedly moist but is not subject to freezing temperatures in winter.

The total area in Mexico occupied by cloud forest is small. The most important distributional unit, and the one most resembling true Andean cloud forest, occurs along the crest of the Sierra Madre de Chiapas. Other sizable belts are in northern Chiapas, along the eastern escarpment from Oaxaca to San Luis Potosí and in the Sierra Madre del Sur of Guerrero. Local, unconnected islands occur on numerous peaks scattered over the Oaxaca uplands and in the Tuxtla range of southern Veracruz.

The montane element of cloud forest usually is dominated by species of pine or oak but may contain many temperate hardwoods of the Appalachian flora such as *Liquidambar, Fagus, Nyssa, Tilia, Cornus,* etc. (Sharp '46). Typical of the understory are tree ferns (that sometimes attain a height of thirty feet), *Podocarpus,* giant *Equisetum,* begonias, bromeliads and orchids along with various species of lianas and other climbing forms. Above Omiltéme, Guerrero, I collected the following additional shrubs that were locally dominant: *Ternstroemia pringlei, Desmodium amplifolium, Verbesina liebmannii,* and several species of *Salvia.*

Tree ferns are perhaps the best plant indicator species. The emerald toucanette (*Aulacorhynchus prasinus*) is a good avian indicator of the type since its distribution in Mexico conforms almost exactly to the area of cloud forest as I have mapped it.

Rain forest

The low, humid tropics are here divided into three vegetational zones—two forest types and savannah. Rain forest has the higher rainfall and more luxuriant growth of gigantic forest trees. Tropical evergreen forest is a little less humid with dense but low stands of broadleaf trees. Along the coastal plains either of these forest types may be broken by patches of savannah. Many elements of fauna and flora occur in all three formations.

Rain forest extends into Mexico from the southeast, halfway up the Yucatán peninsula and along the Gulf coast to southern Veracruz. Lundell ('37) gives an excellent description of the rain forest in northern Petén. Although several hundred tree species are represented, the three largest trees and the species "which characterize the major climatic climax associations in the northern Petén forests" are mahogany (*Swietenia macrophylla*), chicle (*Achras zapota*) and "ramon" (*Brosimum alicastrum*). Of these the chicle is the most characteristic of the whole zone (Lundell '34). Other common tree genera are *Ficus, Bursera, Brosimum, Lucuma, Sideroxylon, Dipholis, Ceiba* and *Cryosophila.* Among the most numerous shrubs are species of *Piper* and *Psychotria.* Palms, lianas, bamboo and a host of epiphytic herbs occur in the understory.

Additional important tree genera in Tabasco and Campeche are *Castilla, Cedrela, Tabebuia* and *Lonchocarpus.*

Tropical evergreen forest

The two principal areas of tropical evergreen forest are the coastal plain and foothills of Veracruz and northeastern Oaxaca and the belt of low forest crossing the Yucatán peninsula between the interior rain forest and the semi-arid tip of the peninsula. The original climax forest has been almost entirely destroyed in Yucatán and greatly reduced in Vera-

cruz, with the result that these areas are now occupied largely by secondary successional stages of scrub forest. In Yucatán the type was probably a dry phase of the chicle forest (Lundell '34) with the mahogany and ramon entirely lacking. The Veracruz evergreen forest, which locally may be almost indistinguishable from true rain forest, is dominated by such tree genera as *Ficus, Cedrela, Cecropia, Enterolobium, Apeiba, Ceiba,* and *Lonchocarpus.* The corozo oil palm or "coyol reál," *Scheelea liebmannii,* is locally abundant as are some other species of smaller palms.

Savannah

Tropical savannah is of limited distribution in Mexico. It is not a climatic climax type of vegetation. Savannahs occur on flat coastal plains or in marshy interior basins, usually as a result of edaphic conditions (poor drainage, etc.) but occasionally as an aftermath to early clearing and cultivation of rain forest or tropical evergreen forest. This formation may appear in the heaviest rainfall belts, as along the coast of Tabasco, or in relatively dry situations such as coastal Nayarit.

The dominant plants are coarse tropical grasses. Scattered trees may occur irregularly spaced over the grasslands, and these are most commonly palms or palmettos. The trees on a coastal savannah in northern Nayarit are palms and calabash (*Crescentia alata*) with figs along watercourses. Nelson and Goldman ('26) list also *Curatella, Coccoloba* and *Byrsonima* as trees that enter the drier savannahs on the Pacific coast.

Tropical deciduous forest

Two principal types of vegetation are presented in the semi-arid tropics: these are, tropical deciduous forest and thorn forest, the latter being the more arid. The main area occupied by these types is the western coastal plain and foothill region, from southern Sonora to Chiapas. In general the thorn forest is coastal, the deciduous forest occupying the more humid foothills below the pine-oak uplands. Smaller areas of deciduous forest exist around the periphery of the arid, interior basin of the Río Balsas and along the borders of tropical evergreen forest in southern Tamaulipas and northern Yucatán. As the name implies, the deciduous forest loses its foliage during the dry period of the year.

Gentry ('46a) calls this type "short-tree forest" and gives an excellent analysis of its composition on a mountain near Culiacán, Sinaloa. On the piedmont, adjoining the thorn forest, some of the dominant plants are *Tabebuia palmeri, Ipomoea arborescens, Bombax palmeri, Bursera laxiflora, Conzattia sericia* and species of *Montanoa, Bursera, Acacia, Cassia* and *Lysiloma.* In canyons a little higher on the mountain are tall forests of *Ceiba acuminata, Bursera arborescea, Lysiloma divaricatum* and *Psidium sartorianum* draped with lianas and various epiphytes.

Another sample of deciduous forest is described by Miranda ('42b) from southwestern Puebla: hillside—*Hauya rusbyi, Coccoloba acapulcensis, Pseudosmodingium perniciosum, Bursera longipes, Bursera morelensis, Conzattia multiflora, Fouquieria ochoterenae, Ruprechtia fusca* and *Cyrtocarpa procera;* alluvial bottoms —*Pithecollobium dulce* and *Prosopis juliflora;* streamside—*Ficus, Salix* and *Taxodium.*

The "Cape forest" of Baja California is quite distinct from the deciduous forest in Sinaloa yet it has little in common with thorn forest (Shreve '37a). H. S. Gentry tells me that this community is most closely related to what he calls "short-tree" forest, hence it is included here. Important species listed by Shreve are *Iatropha cinerea* (dominant), *Lysiloma candida, L. microphylla, Cercidium peninsulare, Pachycereus pecten-aboriginum, Tecoma stans* (dominant shrub), *Viguiera tomentosa, V. deltoidea, Alvordia fruticosa* and *Eupatorium sagittatum.*

Thorn forest

Typical thorn forest in Sinaloa is a dense but scrubby forest, dominated by thorny leguminous trees, particularly acacias. This vegetation type is characteristic of the coastal plains of Sinaloa and Nayarit, continuing down coast at least locally to Acapulco, Guerrero. Other spots of thorn forest appear in Tamaulipas, Veracruz and along the arid coast of northern Yucatán.

Shreve ('34) gives the following list of dominant plants in extreme southern Sonora: *Acacia macracantha* (dominant tree of the forest), *Ichthyomethia mollis, Cercidium sonorae, Ipomoe arborea, Zizyphus sonorensis, Pachycereus pecten-aboriginum, Prosopis glutinosa, Ceiba acuminata, Cassia biflora* and *Coutarea pterosperma.*

Stream bottoms crossing the thorn forest often support high stands of *Brosimum, Ficus* and *Enterolobium.*

Near Ciruelar, Guerrero, the dominant trees are *Acacia cochliacantha* and other legumes of the genera *Mimosa, Caesalpinia* and *Cassia.*

Arid tropical scrub

The Río Balsas valley is a tropical inland basin, cut off from the sea by highlands on all sides. Rainfall is low, and the vegetation is decidedly xeric, resembling cactus desert in some places. Patches of thorn forest and deciduous forest occur locally; certain hills rising from the alluvial plain near Coyuca de Catalán, Guerrero, support a dense bunchgrass association (*Andropogon fastigiatus*). This basin and two smaller ones in Oaxaca are designated as arid tropical scrub.

Typical of the drier hills on the southern edge of the Balsas basin (Cañon de Zopilote, Guerrero) is the organ cactus *Cephalocereus mezcalaensis,* with open thorn scrub in the draws (*Acacia, Mimosa, Caesalpinia*). On slightly more humid uplands near Coyuca de Catalán the following species were found: *Bauhinia longiflora, Zizyphus sonorensis* and *Desmanthus virgatus,* along with the leguminous trees and bluestem bunchgrass mentioned above. *Ficus* and *Taxodium* are typical of streamsides.

MacDougal ('08) lists at Tehuacán, Puebla, *Cereus weberi, Pilocereus tetezo, Fouquieria* and *Prosopis* [*Pithecollobium*] *dulce,* and at Ejutla, Oaxaca, *Cereus* and *Opuntia* on dry sites, *Taxodium mucronatum* and *Ficus* sp. along streams.

Summary

The vegetation of Mexico is here divided into twelve zones, five of Temperate affinities and seven of Tropical, one of which (Cloud Forest) is actually a combination of temperate and tropical elements. The Temperate vegetation zones occupy about 70 per cent of the land area of Mexico. Pine-oak Forest, Mesquite-grassland and Desert are the most extensive types.

Critical winter temperature (freezing) is the principal factor which differentiates the two series, and a rainfall gradient within each series largely determines the zonation into types.

In this classification main vegetational divisions are emphasized rather than details of floristic composition of which only scattered examples are given. Likewise the classification considers only climax types without attempting to designate successional stages resulting from human occupation and disturbance.

The Pine-oak Forest, with its temperate, healthy climate, suitable for the cultivation of corn, has always been the most important zone as regards human populations. Serious impoverishment of vegetation and other natural resources has occurred there as a result of long occupation and unwise agricultural practice.

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BRACKISH WATER PLANKTON OF MANGROVE AREAS IN SOUTHERN FLORIDA[1]

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INTRODUCTION

Scientifically, the waters of the mangrove areas of the world remain practically unexplored. In Florida there occurs one of the most extensive known mangrove areas. Mangrove trees (*Avicennia nitida, Rhizophora mangle* and *Laguncularia racemosa*) cover most of the small keys scattered throughout Florida Bay, as well as the edges of most, and the whole of many, of the Florida Keys. In addition, there is an extensive area several miles wide along the very southern tip of the peninsula proper of Florida, and another equally wide and even more extensive area along the west coast of the southern portion from Cape Romano and the Ten Thousand Islands down to Cape Sable at the southern tip of the mainland. An important portion of this mangrove consocies lies within the boundaries of the Everglades National Park. The distribution of mangroves in Florida has been described by J. H. Davis ('40, '43).

The mangrove areas are broken up by more or less extensive areas of open water, called bays, lakes or sounds according to their location, size, configuration, etc. Most of the bays, lakes and sounds are connected together or to the Gulf of Mexico or the Atlantic Ocean by an intricate system of narrow creeks or wider rivers (estuaries), through which tidal currents flow. For details of the geography of the region see the accompanying map, figure 1.

The authors undertook an exploratory trip through West Lake, Long Lake and The Lungs to Garfield Bight and Florida Bay on June 29, 1947. Samples of plankton were obtained from all of the bodies of water mentioned except The Lungs. The analyses of the samples taken in West Lake and Long Lake were reported by C. C. Davis ('48), while those taken from Garfield Bight and Florida Bay are being reported briefly by C. C. Davis ('50). The only thorough biological explorations of the area were reported by J. H. Davis ('40, '43). In his papers he dealt, however, almost entirely with the flora of the mangrove swamps, and had practically nothing to say on strictly aquatic life. This author ('40, pp. 369–370) is the only one previously to have mentioned the plankton, and he did so only in general terms: "Myriads of small crustaceans and protozoans thrive in the plankton and soils of the swamps." The only other important biological work in the area was that of Henshall ('89), who studied the fishes of parts of Florida Bay. Other authors, among them Carr ('40) and Rathbun ('30), listed individual specimens captured within the confines of the general area. Simpson ('20) described portions of the area through the eyes of a naturalist.

Because interesting results were obtained during the preliminary trip, it was decided to explore the plankton content of these unusual waters more thoroughly. To this end a trip was taken from January 31 through February 2, 1948 to visit the inland bays along the west coast. Subsequently, a second trip was taken during May 1–2, 1948, through the two groups of lakes described above, and through northern Florida Bay, Madeira Bay, Joe Bay and Long Sound.

[1] Contribution No. 42 from the University of Miami Marine Laboratory.

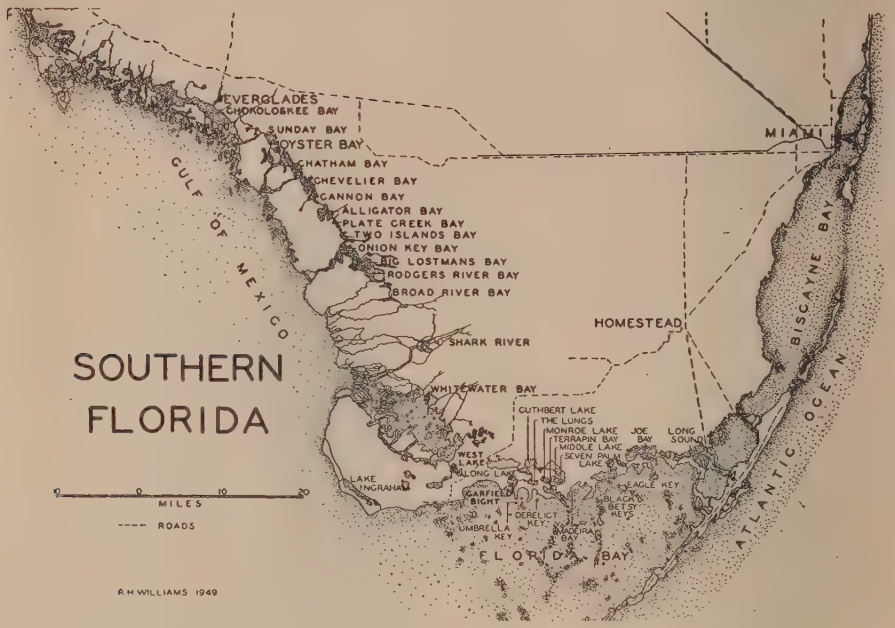

FIG. 1. Sketch map of southern Florida, showing locations mentioned in text.

METHODS

One or more samples of plankton were obtained from each of the larger bodies of water that was visited. Samples were obtained by drawing open twelve inch standard plankton nets behind the skiff while going at low speed. No attempt could be made to standardize the time of towing.

Plankton samples were analyzed by listing the first 200 to 300 organisms of all types encountered. From the figures thus obtained the relative abundance of the various plankton types could be calculated. Results were expressed in terms of percentage of the total organisms. The entire remainder of each sample, without exception, was scanned through a dissecting microscope, and any additional plankton types were listed, in many cases along with a rough estimate of their abundance in the sample. In a few cases of unusual forms, or large forms, the actual number encountered in the entire sample was recorded.

PLANKTON SAMPLES OBTAINED

During the course of the investigations thirty-nine samples of plankton were obtained from twenty-eight localities. In each of the localities a salinity sample was also taken. Table I is a list of the plankton samples, and salinities, to which are added the four samples previously reported upon by C. C. Davis ('48, '50). All samples were taken at the surface.

RESULTS AND DISCUSSION

West coast waters

Most of the drainage of the Everglades is towards the west coast of the peninsula, though some of the drainage also passes southward to enter Florida Bay, and some also passes eastward towards the Atlantic Ocean. The main drainage is indicated in the present results by the relatively low salinities in most of the bays investigated along the west coast, as compared with salinities along the south coast in comparable locations (see table I).

TABLE I.—*Plankton samples obtained from the waters investigated, with salinities*

Sample no.	Date	Location	Net mesh no.	Salinity ‰	Remarks
1	1–31–48	Chokoloskee Bay, off Halfway Creek	20	23.23	
2	1–31–48	Chokoloskee Bay off Halfway Creek	12	23.23	
3	1–31–48	Sunday Bay	20	7.20	
4	1–31–48	Oyster Bay	20	7.68	
5	1–31–48	Chatham Bay	20	7.74	
6	1–31–48	Chevelier Bay	20	9.13	
7	2– 2–48	Cannon Bay	20	4.13	
8	1–31–48	Alligator Bay	20	2.54	
9	2– 2–48	Plate Creek Bay	20	1.40	
10	2– 2–48	Two Islands Bay	20	1.60	
11	2– 1–48	Onion Key Bay	20	3.06	
12	2– 1–48	Big Lostmans Bay	20	3.42	
13	2– 1–48	Rodgers River Bay	20	2.21	
14	2– 1–48	Broad River Bay (upper end)	20	0.61	Mangrove oysters all dead (for a long time)
15	5– 1–48	West Lake (near east end)	20	9.52	
16	5– 1–48	West Lake (near east end)	12	9.52	
*17	6–29–47	West Lake (near middle)	12	18.30	
18	5– 1–48	Long Lake	20	13.28	Much of lake nearly choked with *Ruppia*
*19	6–29–47	Long Lake	12	15.39	No *Ruppia* evident
20	5– 1–48	Cuthbert Lake	20	5.01	
21	5– 1–48	Cuthbert Lake	12	5.01	
22	5– 1–48	The Lungs	20	26.82	
23	5– 1–48	The Lungs	12	26.82	
24	5– 1–48	Garfield Bight near Shark Point	20	29.09	
25	5– 1–48	Garfield Bight near Shark Point	12	29.09	
*26	6–29–47	Garfield Bight, ¾ mi. north of Shark Point	12	26.87	
*27	6–29–47	Florida Bay east of Umbrella Key	12		
28	5– 2–48	Florida Bay, 1 mi. south of Derelict Key	12	27.81	
29	5– 2–48	Seven Palm Lake	20	8.60	Considerable *Ruppia*
30	5– 2–48	Seven Palm Lake	12	8.60	
31	5– 2–48	Middle Lake	20	18.50	
32	5– 2–48	Middle Lake	12	18.50	
33	5– 2–48	Monroe Lake	20	20.32	Lake choked with *Ruppia*
34	5– 2–48	Upper Terrapin Bay	20	25.12	
35	5– 2–48	Upper Terrapin Bay	12	25.12	
36	5– 2–48	Madeira Bay ½ mi. S.W. of Madeira Point	12	27.66	Considerable suspended marl
37	5– 2–48	Florida Bay S. of Little Madeira Bay, 1½ mi. E. of Black Betsy Keys	20	24.92	
38	5– 2–48	Florida Bay, S. of Little Madeira Bay, 1½ mi. E. of Black Betsy Keys	12	24.92	
39	5– 2–48	Florida Bay, N. of Eagle Key	20	24.33	
40	5– 2–48	Florida Bay, N. of Eagle Key	12	24.33	
41	5– 2–48	Joe Bay (about middle)	20	22.56	
42	5– 2–48	Joe Bay (about middle)	12	22.56	
43	5– 2–48	Long Sound, near W. end.	12	25.12	Very short tow

* Samples reported previously (C. C. Davis, '48, '50).

West coast waters are rather completely isolated from the waters along the south coast, for there are no large interconnections by means of canals and creeks. Any temporary water connections during flood periods are across ecologically very distinct regions. Yet all of the west coast waters form an interconnected whole. Chokoloskee Bay, at the northern extremity of the area investigated, is closer

to the open Gulf of Mexico and therefore it had a much higher salinity even though it receives fresh water from three small rivers. South of Chokoloskee Bay, all of the others had relatively low salinities.

The plankton content of the west coast waters is shown in tables II and III. The general sparsity of records of Dinoflagellata among the plants and of Coelenterata, Platyhelminthes and Chaetognatha among the animals is noteworthy. Among the Copepoda, *Temora* sp. and *Metis* sp. were absent from west coast localities though rather regularly found along the south coast. These may, however, have been absent because of the different seasons in which the two regions were investigated. The diatom genus *Pleurosigma* was far more common on the west coast than on the south coast. This also may have been a seasonal difference.

Associated with the higher salinity of Chokoloskee Bay, its plankton differed considerably from that of the other west coast bays. Among the phytoplankters, the most marked difference was the presence of the diatom, *Skeletonema* sp. in fairly large quantities, and the presence of *Rhabdonema* sp. as well. These forms were not encountered elsewhere on the west coast. Among the animals, the lack of rotifers in Chokoloskee Bay served to distinguish its plankton from that of the other bays, as did the presence of such high-salinity copepod species as *Labidocera aestiva* and *Pontella* (?) sp. *Acartia tonsa* occurred only in the sample from here, of all the west coast localities. *A. floridana* also occurred in Chokoloskee Bay, the only case in this study where the two species were found together. Beyond these, the Chokoloskee plankton contained free swimming isopods, amphipods, the larval stages of Macrura and the Paguridae and chordates of various types, whereas other west coast bays were nearly or completely deficient in such forms. The Chordata were represented by nu-

TABLE II. *Plants occurring in samples from west coast inland waters**

Organism	Sample number												
	1, 2	3	4	5	6	7	8	9	10	11	12	13	14
Clathrocystis sp.							76.5	4.0	+				
Merismopedia sp.							4.5	1.0	0.5				5.5
Spirulina sp.						4.0		13.0	11.0				
other blue-green algae	+					5.5		+	2.0		0.5		2.0
Bacillaria sp.		0.5											
Biddulphia sp.	0.5	0.5	+	+								0.5	
Campylodiscus sp.		3.0					+	+	3.0	+	9.5	3.0	11.5
Chaetoceros spp.		+	47.5	59.5	9.0	2.0				0.5			
Coscinodiscus sp.	8.0	1.5	0.5	0.5	+	+	0.5	1.5	1.0	0.5	1.0	+	1.5
Fragilaria sp.			4.0		0.3								
Melosira sp.		+			0.3	1.0				+			
naviculoids	14.0	5.0	2.5	1.5	0.6	12.0	9.5	32.0	40.0	+	3.5	0.5	37.5
Nitzschia closterium	1.5								1.5				
Nitzschia seriata			3.0										
Pleurosigma sp.	5.0	10.0	1.5	4.0	0.6	0.5		0.5	3.5	+	0.5		
Rhabdonema sp.	+												
Skeletonema sp.	8.5												
Tropidoneis sp.						12.0	1.5	+					
Micrasterias sp.													1.0
Sphaerozosma sp.													0.5
Spirogyra sp.							0.5				0.5		22.0
Tetraedron sp.										0.5			8.0
other green algae			5.0						3.5		0.5	+	5.0
Peridinium sp.				0.5									
other dinoflagellates					3.3			0.5					0.5

* All dinoflagellates are included here as plants. Numbers refer to percentage of total organisms. A + sign means the organism was present in small numbers.

TABLE III. *Animals occurring in samples from west coast inland waters**

Organism	Sample number												
	1, 2	3	4	5	6	7	8	9	10	11	12	13	14
Foraminifera	0.5							3.5	0.5	+	1.5	+	1.0
Tintinnopsis spp.	+		1.0	+				0.5		+	5.5	6.5	
other Protozoa		0.5				3.0							
juvenile Hydromedusae					+								
nematodes	+							0.5					
Anuraea sp.		0.5				37.0	1.0	21.5	21.0	18.5	13.0	45.5	
Diplax sp.						0.5							
other rotifers		0.5	+	+		0.5		1.0		+	0.5		1.0
larval polychaetes		+	0.5										
postlarval polychaetes	+	+		+	+	+				+	+		
cirripede nauplius	f.c.	1.0	+	+	+	0.5				+		+	
cirripede cypris		+		(1)						+			
barnacle (metamorphosed)	+												
juvenile cladoceran							(1)	0.5					
juvenile ostracod										+			
copepod nauplii	52.5	66.5	24.5	30.5	67.6	19.0	6.0	18.5	11.0	80.0	54.5	42.5	1.0
Longipedia-type naup.	+												
Acartia floridana	+	0.5	+	+		+			(1)	f.c.	c.		
Acartia tonsa	+												
juvenile *Acartia*	0.5	1.5	1.0	1.0	0.3	0.5			1.0	0.5	1.5	+	
Labidocera aestiva	(3)												
juvenile *Labidocera*	+												
Paracalanus crassirostris					+								
Pontella (?) sp.	(1)												
juvenile calanoid		0.5	+		+	+					0.5		
Oithonina nana	f.c.	0.5	+	+	+					(1)			
juvenile cyclopoid	+									+			+
juvenile harpacticoid	+	0.5		+	+		0.5	+		+	+	+	
mature harpacticoid	+			+		+					+		
Ergasilus versicolor		(3)	(2)										
Ergasilus spp.		+								+	+		
Arguloida	(1)		(1)	(1)							(1)		
isopod	+												
juvenile parasitic isopod (micronisicus)										f.c.			
amphipod	f.c.				+								
macruran mysis	+												
pagurid zoea	+												
brachyuran zoea (long spines)		+	+	+		+				f.c.	+	+	
brachyuran zoea (ordinary spines)	f.c.												
mites					+				+				
gastropod veligers	0.5	0.5	0.5	+	1.6	0.5				+	0.5		
pelecypod veligers	2.5	6.0	9.0	2.5	16.0	1.5		1.0	0.5	0.5	6.5	1.5	
postlarval limpet	+												
tunicate egg	c.												
larval tunicates	f.c.	0.5											
postlarval tunicate	+												
spherical fish eggs	+												
larval fish	+												

* All dinoflagellates are excluded here, regardless of their nutrition. Designations are as in table II. In addition, c. means common, f.c. means fairly common, and numbers in parentheses refer to actual total numbers encountered in the sample.

merous tunicate eggs and larval tunicates, as well as by smaller numbers of fish eggs and of larval fish. The phylum was almost completely missing from the plankton captured at all other west coast locations.

Of the remaining west coast waters, the lowest salinities occurred in Alligator Bay, Plate Creek Bay, Two Islands Bay, Rodgers River Bay and Broad River Bay, while Cannon Bay, Onion Creek Bay and Big Lostmans Bay also had low

TABLE IV. *Plants occurring in samples from south coast inland waters**

Organism	Sample number**																				
	15	17	18	19	20	22	24	26	27	28	29	31	33	34	35	36	37	39	40	41	43
Aphanocapsa sp.					f.c.																
Merismopedia sp.			0.3																		
Skujaella Thiebautii																		+			15.0
other blue-green algae									+			+			3.0						1.5
Campylodiscus sp.												23.0		0.5			46.5	25.0	15.5	25.0	80.0
Chaetoceros sp.						9.3	37.5			39.0	+	2.0	10.5	2.5	10.5	4.0	2.5	1.0	0.5	1.5	+
Coscinodiscus sp.			+			3.3															
Melosira sp.																					
naviculoids	+		9.0	c.		5.0	27.5			0.5	+		2.5	0.5	1.0				1.5		2.0
Nitzschia closterium							2.0														
Pleurosigma sp.			0.3							0.5									2.5		
Rhabdonema sp.							+			2.5											
Tropidoneis sp.						0.3						+									
green algae					+																
Ceratium furca				+		1.0					0.5	2.0	1.0	3.0	1.0		+	1.0	0.5	2.5	+
Ceratium fusus																0.5		+	0.5		+
Dinophysis sp.												+									
Gonyaulax spinifera						+	5.0				47.5	66.0	33.5	23.5		0.5	38.0	64.5	5.5	31.0	+
Gymnodinium sp.												+									0.5
Peridinium sp.	0.3										4.0	0.5	0.5	4.5			3.5	3.5	0.5	5.5	0.5
Prorocentrum sp.																	+				+
other dinoflagellates						2.6	2.5					0.5		3.0	0.5		1.5		1.0		

* All dinoflagellates are included here as plants. Designations are as in tables II and III.

** In those locations where more than one sample was obtained (i.e., with fine net and with a coarse net), the results with the exception of samples 34–35 and 39–40, are given under the sample number of the fine net sample, for this was the only one in which relative numbers were estimated. In such cases, any organisms encountered in the second (coarse) sample that were not found in the other, are indicated above by a + mark, just as in the case of the rarer forms encountered in the fine net sample.

salinities. As might be expected, freshwater types were more abundant here, and typical marine types tended to be eliminated. For example, blue-green algae such as *Clathrocystis, Merismopedia* and others occurred only in the eight low salinity bays mentioned above. Bluegreens were among the dominant organisms, however, only in the freshest bays. Desmids were encountered only in Broad River Bay, which was the freshest of them all.[2]

Juvenile cladocerans (presumably freshwater species) were encountered only in two of the freshest bays. Finally, the copepod genus *Acartia,* so common in Florida marine waters, was absent in four of the five freshest bays, and only a single specimen was found in the fifth.

The bays with somewhat higher salinity (i.e., Sunday Bay, Oyster Bay, Chatham Bay and Chevelier Bay) showed more of the characteristics of Chokoloskee Bay than of the freshest bays, though there was a considerable reduction in the kinds of plankters present. Considering only the fine net sample from Chokoloskee Bay, there was a reduction by about one-third.

South coast waters

The bodies of water that were investigated along the southern coast are all interconnected, at least indirectly. However, West Lake, Cuthbert Lake, Long Lake, Henry Lake, Little Henry Lake and The Lungs all drain into Florida Bay quite separately from Seven Palm, Middle and Monroe Lakes. Madeira Bay and Joe Bay have a drainage into Florida Bay separate from either group of lakes. Long Sound has two connections with Florida Bay, namely, through Rocky Creek at its west end, and through Little Blackwater Sound and Blackwater Sound in the middle. At its east end, Long Sound is also connected indirectly with the Atlantic Ocean through Barnes Sound and Card Sound, and Florida Bay itself

[2] That the bays are subject to wide fluctuations of salinity from time to time is shown by the fact that the shells of dead mangrove oysters were common in Broad River Bay, though its waters were practically fresh.

TABLE V. *Animals occurring in samples from south coast inland waters**

Organism	Sample number (as in table IV)																			
	15	17	18	19	20	22	24	26	27	28	29	31	33	34	35	36	37	39	40	41	43
Foraminifera	(1)			+	+	+	+	(1)	+	+				+	1.0	(1)	+		1.0		
Favella sp.						+														+	
Proplectella sp.														3.0						5.5	
Tintinnopsis sp.						2.6	1.5					3.0		5.5		0.5	1.0	+	0.5	4.5	
other Protozoa											+		1.0								
Obelia medusae						+								+						f.c.	
juvenile hydromedusae			+								+					(1)				+	+
Mnemiopsis sp.		c.	+	+		+	+												+	c.	+
rhabdocoel	(2)		(8)			+					f.c.	+	+	+		(2)	(3)	+		1.0	+
larval polyclad																	+				
Müller's larva																(1)					
nematodes	(1)		(2)				0.5	(1)	+								(2)				
Anuraea sp.					60.0												+				
Brachionus sp.	56.0		33.3		f.c.	6.3					1.5										
Pedalion sp.	30.6		1.6		1.5						+										
Schizocerca sp.					30.5																
Triarthra sp.					f.c.																
other rotifers				+										1.0							
juvenile *Sagitta neglecta* (?)							(1)													+	
juvenile *Sagitta* sp.						f.c.	+	(1)	+	+		+		+	+	c.	+	+	0.5	+	c.
trochophore														+			(1)				
larval polychaete	+					2.6	+				+			+			(1)			c.	
postlarval polychaete						+	+					+		+		(1)		+			+
cirripede nauplius		+						(1)									+		+		
cirripede cypris																					(1)
ostracod					+		+		+												
juvenile ostracod						+				0.5								+	0.5		
copepod nauplii	11.6		20.6	+	4.0	15.3	8.0	+		10.5	15.0	2.0	33.5	25.5	16.0	6.5	1.5	1.5	5.0	11.0	+
Longipedia-type nauplius						0.6	0.5			8.0	+	+	0.5	+	3.0	+	+	+	2.0	0.5	
shed "skins" of nauplii											c.										
Acartia floridana	c.		f.c.	5	c.	0.3					(4)	+	+								
Acartia tonsa							+	c.	c.	1.0				f.c.	+	+	+	f.c.	f.c.	c.	f.c.
juvenile *Acartia*	1.3	+	1.0		1.0	5.6	0.5			1.5	1.0	0.5		1.0	6.0	5.5	0.5		1.0	0.5	
Paracalanus crassirostris												+		+			+	+	0.5		
Pseudodiaptomus coronatus				+																	
Temora sp.						(6)	(2)	c.	+			+	+		(1)						
juvenile *Temora*						+				+		+		+					+		
juvenile calanoid															0.5	1.0	+	+	0.5	0.5	+

TABLE V.—*Continued*

Organism	Sample number (as in table IV)																			
	15	17	18	19	20	22	24	26	27	28	29	31	33	34	35	36	37	39	40	41	43
Oithonina nana						+	0.5			16.5	+	f.c.	1.5	2.0	24.0	46.5	3.0	1.5	14.0	6.0	c.
juvenile *Cyclops* sp.			(2)																		
Cyclops panamensis tannica				95																	
juvenile cyclopoid						3.0		(1)				0.5		+							
Metis sp.							+	+	f.c.	+							+				
juvenile harpacticoid											+			+					+		+
harpacticoid indet.						+		(3)	+						(1)						
Ergasilus versicolor					(3)																
Ergasilus spp.	+									+											
Arguloida											+										
Caligoida						(2)		(2)	(3)	(1)					(3)						
Isopoda							f.c.		+	f.c.						(4)					
juvenile parasitic isopod (microniscus)										+											
Amphipoda							+	(1)	+												
caprellid							+														
macruran zoea											+							+			
macruran mysis	+	(1)	(1)		(3)	c.	+		+	c.		+		+	+				+	+	
shrimp with eggs							(1)														
pagurid zoea										+						+	+				
brachyuran zoea (long spines)	+		(4)	+?	c.	0.3						+									+
brachyuran zoea (ordinary spines)							(1)	f.c.?	+?	c.				+	+	(4)	(4)	+	+	+	+
mite											+										
dipteran larva							+				+										
gastropod veliger	+		30.3		0.5	3.6	6.5	(1)	+	16.5			0.5	1.5	14.0	28.5	+	1.0	33.5	1.5	0.5
postlarval gastropod					(17)	+										(2)					
postlarval nudibranch																			+		
Ostrea veliger																					+
pelecypod veliger	+		3.3		2.5	39.6	7.5		+	5.5	30.5	+	15.0	23.0	19.5	2.5	1.0	1.0	13.5	3.5	+
postlarval pelecypod																(1)					
echinopluteus																					+
appendicularian															(1)	1.0	c.	c.	0.5		+
oval fish egg						+						+				c.	+		+	+	+
spherical fish egg	c.	c.	(10)	+		+		c.?	+?	c.		+	+			+	+	+			
postlarval pipefish							+														
larval fish	(2)	(1)			(13)	+	+	+	+	c.	+	+	+		(1)		(2)	+		+	+

* Dinoflagellates are excluded here, regardless of their nutrition. Designations are as in tables II and III.

has numerous connections with the Atlantic Ocean through the openings between the several Florida Keys. Florida Bay is continuous with the Gulf of Mexico along its western periphery.

Salinities were in general higher in the south coast bodies of water than along the west coast. They were, however, lower in the lakes, than elsewhere, because of the more concentrated effect of drainage. In both groups of lakes, the lakes farthest from Florida Bay were by far the freshest, and these compared in their salinities with west coast localities (see table I).

Tables IV and V show the plankton content of samples collected in south coast waters. The south coast samples in general were characterized, compared with those from the west coast, by the sparsity of records of blue-green algae, exclusive of the marine *Skujaella* (*Trichodesmium*) *Thiebautii,* by the complete lack of desmids, and the practical absence of green algae, as well as by the much smaller quantities of *Pleurosigma* encountered. In addition, among the plants, there was a much better representation of the Dinoflagellata. Among the animal forms, Coelenterata, Ctenophora, Platyhelminthes, Chaetognatha and Chordata were well represented. Other differences, possibly seasonal, were described above.

The plankton of the western group of lakes reflected the relative isolation of the lakes in a number of ways. Many forms that were regularly found in other south coast localities were seldom or never found in these lakes. This was the case, for example, with the diatoms *Chaetoceros* sp. and *Coscinodiscus* sp., with the Dinoflagellata, especially *Gonyaulax spinifera* (?),[3] with *Tintinnopsis* spp., and other tintinnids, with *Longipedia*-type copepod nauplii, and with the copepods *Temora* sp., *Metis* sp. and *Oithonina nana.* On the other hand, rotifers of various kinds were very common in the lakes of this series, but were hardly found at all in other south coast localities.

Acartia floridana was originally described from Long Lake, one of this group of lakes. In the present study it was encountered again in the type locality, and in addition was found in all the other lakes of the group. The species, however, was not confined to the lakes of this group, but was encountered also in all of the lakes of the other group, as well as in many of the bodies of water investigated on the west coast where, however, it did not occur in the waters with the lowest salinities. The species occurred only in the more enclosed and isolated waters, and was replaced by *A. tonsa* in more open waters such as Florida Bay, Madeira Bay, Joe Bay and Long Sound. The two species are very similar to each other, and it is the author's opinion that *A. floridana* evolved from *A. tonsa* through isolation in the special environment of the nearly enclosed mangrove swamp bays and lakes.

Pagurid zoeae of Brachyura were encountered frequently, and they were especially common in Cuthbert Lake, which had the lowest salinity of all south coast localities. However, the brachyuran zoeae encountered in the lakes were entirely different from those found in other south coast waters except Middle Lake and Long Sound. The dorsal and lateral spines of the carapace were extremely long. This zoea was the same as those that were encountered in many of the west coast localities investigated. The species of crabs living in the mangrove swamps are limited, and it should not be difficult to determine the species to which this zoea belongs. It has no resemblance to the zoea of the fiddler crab (*Uca minax*), as described by Gray ('42), nor was it a porcellanid.

The plankton of the individual lakes of the series differed considerably from each other. The Lungs, with its high salinity and close proximity to Florida Bay, showed many transitional characteristics. The plankton from The Lungs was simi-

[3] Tentatively identified by Dr. G. W. Prescott, of Michigan State College.

lar to that of the other lakes in the presence of *Acartia floridana* and long-spined brachyuran zoeae, in the practical absence of *Gonyaulax spinifera* (?), and in the presence of relatively large numbers of rotifers. Smaller numbers of rotifers, however, were present here than in the other lakes. On the other hand, the plankton was similar to that of other south coast waters in the presence of *Coscinodiscus* sp., *Tintinnopsis* sp., juvenile Chaetognatha, *Longipedia*-type nauplii, *Temora* sp., etc.

The other lakes showed some peculiarities, apparently based primarily on salinity differences. Cuthbert Lake had the lowest salinity, and it was here that the rotifers were almost abundant, constituting 92.0 per cent of the total organisms. There were five genera of rotifers represented, of which three were not found in any of the other lakes. The most common rotifer was *Anuraea* sp. (60.0 per cent of the total organisms). In West Lake, where the salinity also was fairly low, rotifers constituted nearly 87 per cent of the total organisms. In Long Lake, where copepod nauplii and gastropod veligers were of much greater importance than elsewhere, the rotifer population was smaller, though they were still very common.

West Lake and Long Lake had been investigated ten months previously (C. C. Davis, '48). There was a great difference in the salinity of West Lake. However, there was little change in the salinity of Long Lake. The plankton content of the waters was very different in both cases. In West Lake in June, 1947, Ctenophora of an unidentified species dominated the plankton almost to the exclusion of other plankters. The species is now thought to have been *Mnemiopsis* sp., for that genus is the only one subsequently encountered in the area. In Long Lake, copepods dominated the plankton: (*Cyclops panamensis tannica,* 95 per cent; *Acartia floridana,* 5 per cent; *Pseudodiaptomus coronatus* present in small numbers). In 1948, in West Lake, rotifers were dominant, while in Long Lake they shared their dominance with other forms (as indicated above.) Of the copepods found in Long Lake in 1947, only *Acartia floridana* was found in 1948, though two immature specimens belonging to the genus *Cyclops,* possibly *C. panamensis tannica,* were found.

In the second group of south coast lakes, consisting of Seven Palm, Middle and Monroe Lakes, the plankton showed great similarity to that of the more open waters of Florida Bay, Madeira Bay and Joe Bay, except in the absence of *Ceratium fusus* and of short-spined brachyuran zoeae, and in the presence of *Acartia floridana.* The waters of these lakes also showed a surprisingly small number of gastropod veligers, though these forms were very common, or even dominant in most of the other waters investigated both on the west and south coasts, aside from the freshest waters on the west coast. There was no corresponding deficiency in the quantities of pelecypod veligers.

The waters of Florida Bay, Madeira Bay, Joe Bay, and Long Sound were in general of a higher salinity than those of the more inland bodies, though distinctly brackish. It was only in these waters that *Skujaella* (*Trichodesmium*) *Thiebautii, Rhabdonema* sp., *Ceratium fusus, Prorocentrum* sp., *Proplectella* sp., *Obelia* medusae (as an exception, a few of these were found in The Lungs), *Acartia tonsa, Temora* sp. (some *Temora* were encountered in The Lungs), *Metis* sp., isopods, amphipods, short-spined brachyuran zoeae, appendicularians and oval fish eggs (similar to anchovy eggs) were found.

During 1947, plankton samples were taken from Garfield Bight and from Florida Bay near Garfield Bight. These are being reported briefly by C. C. Davis ('50), but a more detailed report is given here. The salinity was determined in 1947 for the water at a point somewhat closer to the head of the bight than was the case in 1948, and therefore the higher figure for 1948 may not be completely comparable. As in the 1948 samples

prominent plankters were *Temora* sp. and *Metis* sp.

Abundance of larval forms

Certain interesting facts characterized the distribution of the larval stages of certain pelagic species. Most striking was the case of the Chaetognatha, whose immature stages were sometimes common, though no adult individuals were encountered in any of the samples. The larval stages were almost always so extremely immature that it was impossible to ascertain to which adult species they belonged. The same phenomenon has been observed previously in Florida waters (C. C. Davis, '50) with respect to the chaetognaths. Davis found that their immature larval stages often occurred in localities far removed from any water that could be considered to be the natural habitat of the adults.

Florida Bay as a whole is very shallow, and hardly seems suitable for the growth to adulthood of chaetognaths, though the presence of larval stages is an indication either that adults occur at times, or that eggs drift in from outside. Possibly, as has been shown in the case of copepods (see below), the chaetognaths of the hardy species involved [4] are able to live during unfavorable conditions in the larval sages, and then mature rapidly when favorable conditions develop.

The distribution of immature stages of copepods was similar, though not quite so striking. In the bays on the west coast the water was probably abnormally low in salinity. Not many adult copepods were encountered, as compared, for example to the sample obtained from Long Lake on the south coast the previous year. Yet copepod nauplii were often extremely common. Farran ('27) and Nicholls ('33) have shown that *Calanus finmarchicus* remained in the immature 4th and 5th copepodid stages during the winter months, and then quickly matured in the spring, presumably because of the spring food or temperature conditions. Coker ('33) discussed the arrest of development of an undescribed copepod from North Carolina, which spent long periods in the 4th copepodid stage and would advance to maturity only when environmental temperatures were greatly reduced. Possibly the species of copepod inhabiting the waters of the area investigated carry over during unfavorable periods in their juvenile stages, and develop to maturity only when suitable environmental conditions develop.

Parasitic copepods

Free-swimming individuals of parasitic copepods were unusually common in the samples investigated, both on the west coast and the south coast. A species that was nearly identical with *Ergasilus versicolor* was obtained in small numbers in samples from Sunday Bay, Oyster Bay and Cuthbert Lake. To the best of the authors' knowledge, *E. versicolor* has not previously been reported from salt water. It is known to parasitize catfish in several North American fresh-water lakes. Other species of the genus *Ergasilus* were encountered in a number of the samples. Arguloids were found in the samples from Chokoloskee Bay, Oyster Bay, Chatham Bay, Big Lostmans Bay, and Seven Palm Lake. Caligoids, some of them mature, were found in The Lungs, Florida Bay south of Derelict Key, and Terrapin Bay. Caligoids were also prominent in the samples obtained in 1947 from Garfield Bight and Florida Bay. None were encountered on the west coast.

Tychopelagic species

Tychopelagic species are listed in the tables. The samples in which the most striking occurrences of tychopelagic species were noted were from Chokoloskee Bay, from the very shallow Garfield Bight, and from Florida Bay north of Eagle

[4] The few individuals of sufficient age to recognize belonged to the species tentatively identified by C. C. Davis ('50) as *Sagitta neglecta* (?), which has been found in the adult stage in certain inland waters, such as Biscayne Bay.

Key. In no case could the net have scraped the bottom, but in a number of localities, including some of those mentioned, there was a good deal of turtle grass floating on the water, in which the forms in question might have been hiding.

Conclusions

The data obtained suggest three major influences of importance in the determination of the nature of the plankton population, namely, seasonal influences, the effect of isolation and the effect of salinity differences. Of these, little is shown of the importance of seasonal (temperature, light, etc.) influences, due to the limited seasonal distribution of the samples obtained. On the other hand, the influence of isolation is clearly shown. Thus, on the south coast, where no seasonal influence could have been operating, the plankton of West Lake (salinity 9.52°/₀₀) was very rich in rotifers and poor in pelecypod veligers, while in the plankton of Seven Palm Lake (salinity 8.60°/₀₀) pelecypod veligers were very numerous and rotifers were relatively rare. It is to be expected that where the biological history of bodies of water differ, due to isolation from each other, their faunas and floras will differ widely, even though chemical and physical environmental factors are very similar.

Perhaps of greatest significance, however, were the salinity differences. The waters in question not only differed greatly from each other in salt content, but each body of water evidently changes considerably in salinity from time to time. Desmids, most blue green algae and green algae were confined to the freshest bodies of water, while the abundance of rotifers was inversely proportional to salinity. Yet the bodies of water which were fresh or nearly so when examined, at other times would have a proportion of salt sufficient to kill such organisms. It is clear that fresh-water plankters regularly are eliminated by increasing salinities and that they must reinvade the territory each time conditions again become favorable.

On the other hand there is the problem of marine species adapting themselves to brackish-water conditions. The fresher the water, the more marine species are eliminated, and such forms periodically must restock depleted waters when higher salinities again are attained. It is thought, however, that many such forms, especially chaetognaths and copepods, are able to tide over the unfavorable period in immature or larval stages.

Summary

1. A total of 39 plankton samples from 28 mangrove-bordered, inland bodies of water along the lower west coast and the south coast of the peninsula of Florida were analyzed. Salinity was also determined from each locality. Biologically similar ecological areas have hardly been investigated previously anywhere in the world.

2. Salinities varied from 0.61°/₀₀ in Broad River Bay (i.e., nearly fresh) to 29.09°/₀₀ in Garfield Bight off Florida Bay.

3. West coast localities were found to differ from south coast localities in their plankton content, probably primarily due to isolation.

4. On the west coast, Chokoloskee Bay, with high salinity, contained more species than other west coast localities, and the species were more of the oceanic type than those elsewhere. The five bays with the lowest salinities contained a good proportion of fresh-water types. Bays with intermediate salinities were more closely similar to Chokoloskee Bay than to the fresher bodies of water.

5. On the south coast, the plankton content of the open Florida Bay and similar bodies of water differed from that of the more enclosed lakes in many respects. The lakes are isolated by independent drainage systems into two groups, and this fact was clearly shown in specific plankton differences.

6. Within each group of lakes differences of plankton content occurred. These

differences probably were associated most closely with salinity differences.

7. Free-swimming parasitic copepods, tychopelagic species, and abundant larval forms were encountered.

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MICROCLIMATIC VARIATION IN A SMALL VALLEY IN EASTERN TENNESSEE [1]

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The environmental differences which obviously exist between adjacent and contrasting habitats in hilly or mountainous country, and which account for slope differences in the vegetation, are of perennial interest. The study here reported represents an attempt to measure the magnitude of temperature differences on opposing north- and south-facing slopes of a typical small valley, with particular reference to variability, seasonal trend, frost pattern, and actual freezing damage to experimental plants at the seedling level.

The vegetation pattern of hill country within the deciduous forest region indicates an exceedingly complex pattern of local environment. Contrasting vegetation, in which no one species is a dominant on both slopes, commonly characterizes the opposite slopes of east-west valleys or ridges. Frequently certain species may be entirely restricted to one slope or the other. Topography and direction of slope are of such importance as site factors that they are coming to be used as major criteria in species selection for reforestation, as in the detailed recommendations of Minckler ('46) for old field planting and interplanting in the Appalachian Valley.

In regions of moderate to strong relief the range of variability with respect to certain environmental factors is apparently so great that the limits of tolerance of certain species with respect to those factors are exceeded on certain sites. These extreme sites are therefore not a part of the "potential areas" of such species (Good '47). Even if all competition were eliminated, such species would not occupy the entire area.

Hill country, therefore, affords an opportunity to study side by side contrasting environments in which a species can or cannot occur. In such a situation inferences concerning causal or correlative relationships of measurable environmental factors to the vegetation may be checked, and in this way the elusive problem of quantitative measurement of effective environment may be approached.

THE STUDY AREA

A small east-west valley (fig. 1) of moderate relief, adjacent to the eastern edge of the Cherokee Farm of the University of Tennessee Experiment Station, about one mile south of the city limits of Knoxville, was selected for detailed study.

This area combines several desirable features. The entire small watershed is covered with unpastured natural vegetation, a remnant of the original forest cover. It is readily accessible but reasonably free from casual visitors. The average direction of the axis of the valley is 15 degrees south of west and the valley is essentially symmetrical in cross section with slopes sufficiently steep that winter sun is tangent to the north-facing slope, and summer sun is perpendicular to the south-facing slope (fig. 2). The degree of relief and the vegetation contrasts are essentially typical of that portion of the great Appalachian Valley centering at Knoxville. The upland area is underlain with the Tellico sandstone and the soils, which belong to the Tellico series, are relatively uniform throughout the area.

The axis of the small valley studied is occupied by a wet weather stream which remained dry throughout the period here reported. At station 1 it is tributary to a swampy flat-bottomed valley, about 100 feet wide at this point, which is drained through a limestone sink about 100 yards to the northwest. Since this drainage area has no valley outlet, cold air which

[1] Contribution from the Botanical Laboratory, The University of Tennessee, N. Ser. 117.

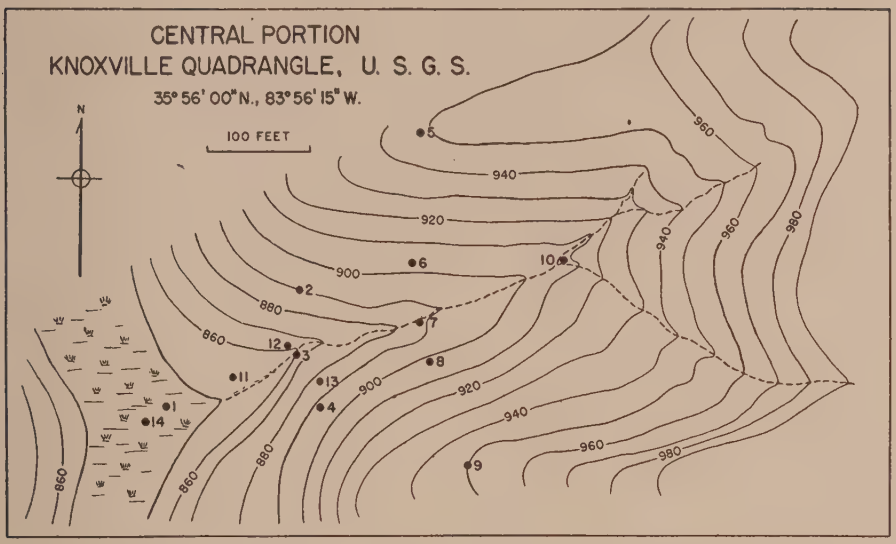

FIG. 1. Station locations in relation to the topography of the study area.

drains into the valley flat from higher levels must necessarily accumulate on quiet nights.

The results of detailed sampling of the upland vegetation by means of a belt transect 20 meters wide, and parallel 1 × 10 meter ground cover plots at 5 meter intervals are reported elsewhere (Jackson '49). These data show that about half the species are not obviously restricted to the south- or to the north-facing slope, but at the same time indicate restriction in distribution of certain species in all layers of the vegetation, and warrant the recognition of two contrasting association-segregates (Braun '35) within an interrelated mixed mesic to sub-xeric complex. The ridge tops and south-facing slope are characterized by one of these segregates, to which are restricted the following typical species:

Quercus coccinea [2]
Q. alba
Carya glabra
C. tomentosa
Diospyros virginiana
Vaccinium stamineum
V. vacillans
Ceanothus americanus
Lespedeza intermedia
Coreopsis major
Desmodium rotundifolium
Lespedeza procumbens
Viola triloba

The north-facing slope and valley bottom are characterized by a contrasting association-segregate and the following species are restricted to it:

Fagus grandifolia
Liriodendron tulipifera
Fraxinus americana
Staphylea trifolia
Hydrangea arborescens
Rhus radicans
Smilax tamnoides var. *hispida*
Adiantum pedatum
Polystichum acrostichoides
Hepatica americana
Tiarella cordifolia
Solidago caesia
Cimicifuga racemosa

A number of wide-ranging species occur rather generally in both association-

[2] Plant names follow the usage of *Gray's Manual of Botany*, eighth edition, 1950.

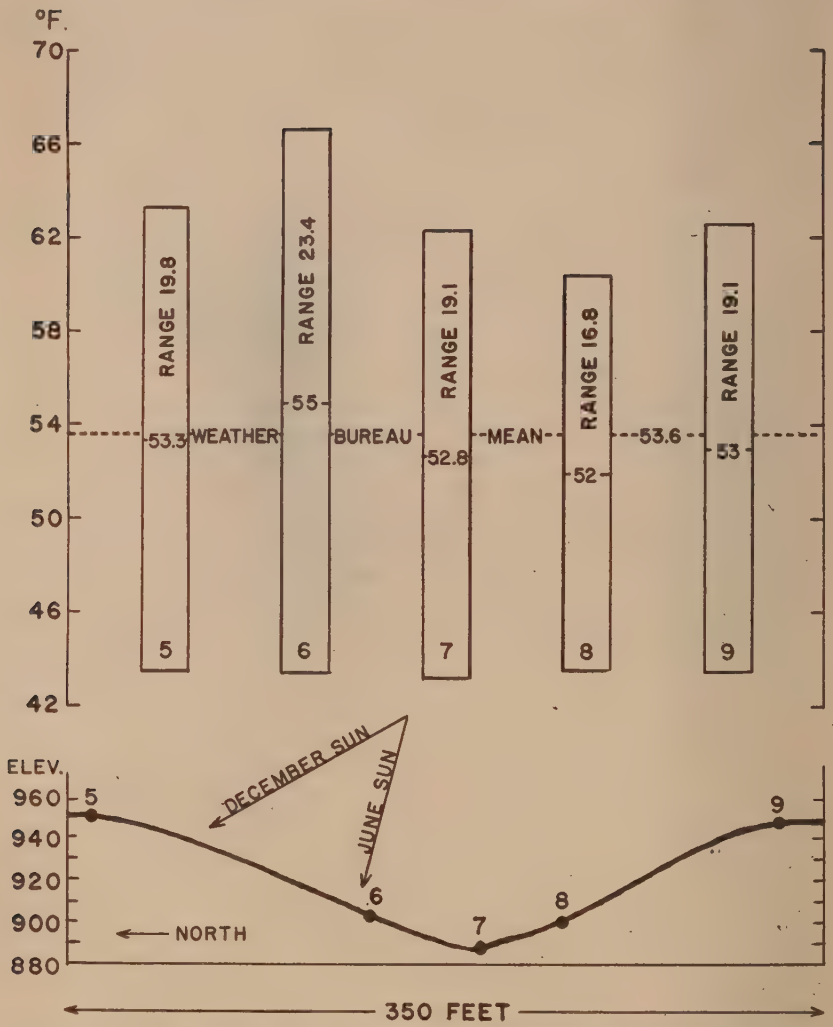

FIG. 2. Cross section profile of valley with no vertical exaggeration, with mean temperatures and mean temperature ranges for the stations indicated for the period October 27–November 13, inclusive, 1947.

segregates and make it difficult to establish definite boundaries between them. These binding species, some of which occur in each layer of the vegetation, include the following:

Nyssa sylvatica
Prunus serotina
Acer rubrum
Oxydendrum arboreum
Sassafras albidum
Ulmus alata
Cornus florida
Viburnum rufidulum
Vitis aestivalis
Smilax glauca
Chimaphila maculata
Desmodium nudiflorum
Eupatorium rugosum
Sanicula marilandica

Methods

Since temperature stands in a key relationship to several other environmental factors, and influences all life processes, it received primary attention in the studies here reported. These initial temperature studies were made in October and November, 1947. They were in part continued during the fall of 1948 in a study primarily concerned with soil moisture trend and pattern (Jackson '49).

Maximum-minimum thermometers (Taylor Instrument Company—Six's type with plastic backs) were mounted on $\frac{3}{8} \times 3 \times 12$ inch boards and placed so as to face north one foot above the substrate. The mountings permitted free circulation of air about the thermometer bulbs and prevented exposure to direct insolation. Temperatures were recorded at almost daily intervals. The ten stations initially established (fig. 1) were arranged so as to constitute a 413 foot east-west profile of the valley bottom (stations 1, 3, 7, 10) and two north-south transects of the valley perpendicular to that profile (stations 2, 3, 4; stations 5, 6, 7, 8, 9). The longer of the two crosswise transects, indicated in figure 2, was 329 feet in length. Four additional stations (numbers 11 to 14) were later established. Extremes of elevation at the stations were 850 and 950 feet.

This method of measurement sampled within the ground layer of herbaceous vegetation, a layer through which the seedlings of the dominant woody plants must pass in the most critical period of their development. It provided data which would be comparable with those of the study by Wolfe, Wareham, and Scofield ('43, '49) and satisfied the requirements that the installations be as simple and inconspicuous as possible.

Tomato plants were installed at stations 1–10 on November 6 and at stations 11–14 on November 8. Four-inch greenhouse-reared plants of the Marglobe variety, in three-inch pots, were used. Plants were not removed from the pots, except in one case, but were set with the pots flush with the soil surface. In the single case (station 13), the plant was removed from the pot and set into a niche in a north-facing limestone outcrop in a habitat characterized by *Sedum ternatum* and *Hepatica americana*. The plants were well-watered when set out and at one later date between rains to keep the soil above the wilting point.

Mean Temperature Pattern

Figure 2 summarizes temperature conditions across the valley for a sample eighteen-day period. This period includes the first two occurrences of freezing temperatures in the area, on one of which occasions detailed all-night observations were made. Means were obtained by adding maxima and minima and dividing by two. Although this procedure may be subject to certain errors (Baum '49) it is a method commonly used and the only method which could be used with the present data.

Presentation of these data as means calls attention to the consistent differences between north- and south-facing slopes in means and mean ranges which result from the differences in maximum temperatures. The other three stations shown are quite similar in pattern and for this period resemble the official Knoxville record, taken in a standard shelter at the Knoxville Municipal Airport nine miles away.

The 3° F mean difference between stations at the same elevation on opposite slopes of the valley is the order of temperature difference which might occur between stations of similar direction and angle of slope and topographic position differing in altitude by 950 feet (Peattie '36) or in latitude by 200 miles (Baum '49).

A further comparison of the stations on this transect is made in table I, which summarizes temperature extremes for the same eighteen-day period. These data show range of variability at the stations and are consistent with the generalizations of figure 2.

TABLE I. *Temperature extremes in degrees F for the period October 27–November 13, inclusive, 1947*

Station	Maximum	Minimum
5	77.0	30.5
6	79.0	29.5
7	76.0	30.0
8	75.5	29.0
9	77.0	30.5
USWB	76.0	31.0

FALL TEMPERATURE TREND

The sharp downward temperature trend for the same fall sample period is illustrated in figure 3, which is based on daily maximum and minimum temperatures for the two most different stations in the longer cross section profile. The successively lower minima as each active cold front brings winter nearer are strikingly evident, as are the intervening periods when rainy weather damps the extremes,

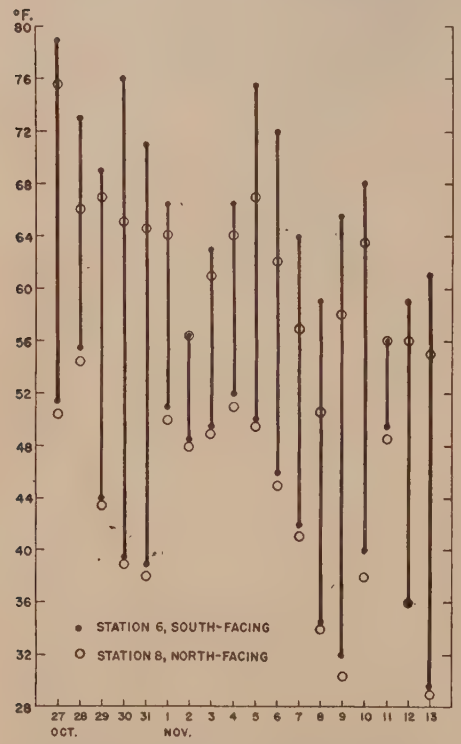

FIG. 3. Fall temperature trend as indicated by daily maximum and minimum temperatures on opposing slopes for the period just preceding and including the first killing frosts.

greatly reducing both insolation and reradiation (November 2 and November 11). Except on these occasions the south-facing slope has consistently the higher maxima of the two, the difference reaching 11° on October 30. Except for November 12 when no difference exists the north-facing slope has consistently the lower minima, but the difference does not exceed 2° and is usually 1° or less.

Frost was first observed in the vicinity of Knoxville on November 6, but no frost occurred in the study area that morning and the lowest temperature recorded was 34°. Two mornings later, on November 8, frost occurred in the valley flat near station 1 and was still evident in the shadows at 9:25 A.M. On that date the first freezing temperature was also recorded in the study area, a minimum of 32° at the one-foot level at station 1.

On November 9 the freezing line included all the profile stations below the ridge tops, and on November 13 went over the top, with minima ranging from 28.5 to 30.5°. The official U. S. Weather Bureau station reported a minimum of 31° on November 13, and designated this date the official "first killing frost."

FROST PATTERN AND FREEZING DAMAGE

As the fall season progressed it was evident that on quiet nights minimum temperatures varied in a topographic pattern which resulted from cold air drainage as well as radiation differential. It was therefore predicted that stations would differ in duration of freezing temperatures as well as in minima.

To check on duration of freezing temperatures, all-night observations were made on the night of November 8–9. The weather on November 8 was clear and cool. Maximum temperatures had become progressively lower during the preceding three days, and scattered light frost was predicted for the area.

As a check on actual freezing damage to plants and its correlation with recorded temperatures, the tomato plants which had

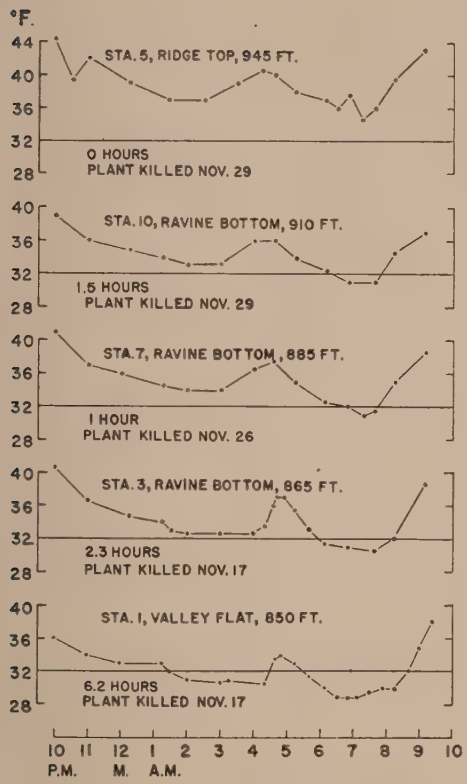
°F.
STA. 5, RIDGE TOP, 945 FT.
0 HOURS
PLANT KILLED NOV. 29
STA. 10, RAVINE BOTTOM, 910 FT.
1.5 HOURS
PLANT KILLED NOV. 29
STA. 7, RAVINE BOTTOM, 885 FT.
1 HOUR
PLANT KILLED NOV. 26
STA. 3, RAVINE BOTTOM, 865 FT.
2.3 HOURS
PLANT KILLED NOV. 17
STA. 1, VALLEY FLAT, 850 FT.
6.2 HOURS
PLANT KILLED NOV. 17
10 11 12 1 2 3 4 5 6 7 8 9 10
P.M. M. A.M.

FIG. 4. Temperature pattern at one foot level, with total hours of freezing temperature for the night of November 8–9, and dates of death of tomato plants exposed at these stations. Location of the stations is shown in figure 1.

been installed at the stations were also observed at frequent intervals.

The stations for which data are presented in figure 4 constitute a related topographic series (fig. 1). The obvious relationship of temperature to altitude is interpreted as resulting from the flow of the cooler, and therefore denser, air down-valley and its accumulation at the lower stations. The freezing line moved progressively up the valley from station 1 past station 3, but there is some evidence that station 10 was situated in a slight frost pocket, where freezing temperatures occurred a little sooner and lasted a little longer than at station 7. On this particular night the freezing line ascended the 60 feet difference in altitude between stations 1 and 10 in about 5 hours. Freezing temperature was not recorded at the ridge top stations.

The more erratic pattern of station 5 was due to disturbance by very slight breezes at this exposed ridge-top station. Only once was a breeze noticed in the valley bottom. At 4:20 A.M. a perceptibly warm down-valley breeze of sufficient force to rustle the leaves was apparent. It progressively affected the stations from top to bottom of the series shown in figure 4, resulting in considerable mixing as far down as the one-foot level in the valley flat (fig. 5). This disturbance subsided in less than half an hour, the marked temperature inversion was quickly reestab-

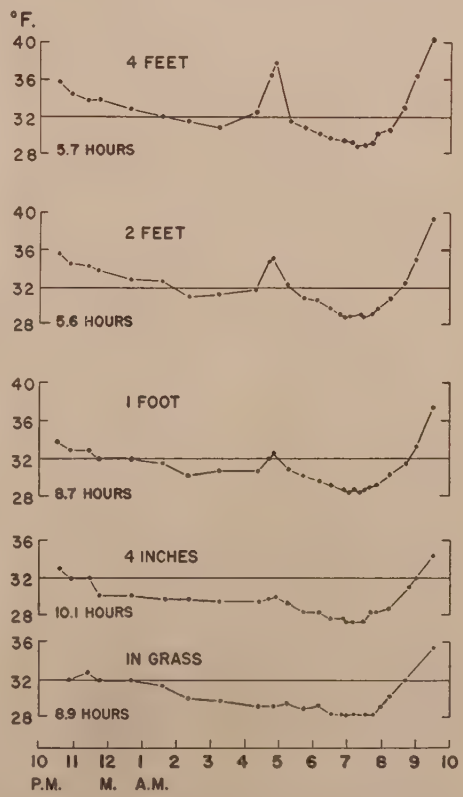

FIG. 5. Vertical temperature profile at station 14 in the valley flat for the night of November 8–9, with total hours of freezing temperature at each level.

TABLE II. *Summary of minimum temperatures in degrees F, dates of death of tomato plants, and duration of freezing temperature on a sample night*

Station number	Description	Ft. elev.	Minimum temperatures, ° F					Date of death of tomato plants	Hours freezing temp., night of Nov. 8–9
			Nov. 8	Nov. 9	Nov. 13	Nov. 17	Nov. 26		
1	Valley flat	850	32.0	28.8	28.5	28.0	26.0	Nov. 17	6.2
2	South-facing slope	890	35.0	32.0	30.0	31.0	28.0	Nov. 26	1.0
3	Ravine bottom	865	33.0	30.5	29.0	29.0	26.5	Nov. 17	2.3
4	North-facing slope	895	33.5	30.0	28.5	29.0	26.0	Nov. 26	1.1
5	Ridge top	945	36.0	34.5	30.5	33.0	29.0	Nov. 29	0
6	South-facing slope	905	34.5	32.0	29.5	30.0	28.0	Nov. 26	0.5
7	Ravine bottom	885	34.5	31.0	30.0	30.0	28.0	Nov. 26	1.0
8	North-facing slope	905	34.0	30.5	29.0	29.5	27.0	Nov. 26	1.5
9	Ridge top	950	35.5	34.0	30.5	32.0	28.0	Nov. 26	0
10	Ravine bottom, pocket	910	34.0	31.0	29.5	30.0	28.0	Nov. 29	1.5
11	Mouth of ravine	855		30.8*				Nov. 17	5.0*
12	Under edge of rock ledge	865		34.0*				Nov. 29	0
13	North-facing rock outcrop	885		32.9*				**	0
14	Valley flat	850		28.1				Nov. 9	8.7

* At 4 inch level, temperatures from unshielded laboratory thermometers.
** Cause and date of death uncertain.

lished and the freezing line again moved up the valley past station 7 by 6:50 A.M. Minima at the various stations occurred between 6:30 and 7:40 A.M.

Hours of freezing temperature during the night of November 8–9 are recorded for each of the stations in figure 4 and for each level of the vertical profile at station 14, summarized in figure 5. The data of figure 5 were obtained from unshielded laboratory thermometers.

The only tomato plant killed on this night (November 9) was at station 14, in the valley flat. The temperature at the level of the tomato plant here was the coldest recorded in the entire area, reaching a minimum of 27.3° from 7:00 to 7:30 A.M. Frost was first observed on dead leaves about this station at 11:00 P.M. Freezing temperatures had been recorded five minutes earlier both in the grass and at four inches, among the leaves of the tomato plant. The temperature had dropped to 30.2° by 11:45 P.M. and did not rise above this level until about 8:30 A.M. The plant was apparently killed by 3:15 A.M., after 3.5 hours at about 30°, and only 4.3 hours below 32°. The plant in the valley flat at station 1 sustained some damage but was not killed, although 2 hours at 30° and 6.2 hours below 32° were recorded at the one foot level, as contrasted with only 2.5 hours and 8.7 hours, respectively, at the one foot level at station 14, where the plant was killed.

Three of the remaining tomato plants were killed on November 17, six on November 26, and the last three on November 29 (table II). In general, each succeeding and harder freeze extended a little farther up the valley. The four dates of death cover a range of from 4 days before to 16 days after the U. S. Weather Bureau "date of first killing frost," and indicate that in 1947 the micro-habitats of this typical small valley differed by at least 20 days in length of the fall portion of their potential growing season.[3]

The minimum temperatures on days when frost occurred (table II) show much less precise correlation with date of death of the tomato plants than do the data on duration of freezing temperature. The low temperatures recorded at all but the ridge top stations on November 13 would have been adequate to cause the death of the plants if they had lasted for a long enough time. The tomato plants on the

[3] In 1948 the range of dates of "first killing frosts" as indicated by death of tomato plants in similar situations was at least 46 days (Jackson '49).

north-facing slope again survived temperatures of 29° and 29.5° on November 17. These observations illustrate and emphasize the fact that time is required for the heat transfer which must precede the freezing of plant tissue as pointed out by Shreve ('11). A critical air temperature must be attained and maintained for a period of time before a critical tissue temperature can be reached.

Summary

A typical small valley near Knoxville, Tennessee was studied with reference to fall temperature pattern and trend, frost pattern and actual freezing damage to tomato plants which were used as phytometers. The area was occupied by unpastured natural vegetation, with contrasting association-segregates on the opposing north- and south-facing slopes.

Temperatures recorded by maximum-minimum thermometers at the one foot level indicated an erratic but sharp downward temperature trend in all micro-habitats studied, with maximum contrast on clear days which followed the advent of each cold air mass. During a sample fall period mean temperatures differed by 3° F across the valley, chiefly as a result of differences in the maxima.

Critical differences in minimum temperature occurred among the micro-habitats studied, the difference between extreme ridge top and valley flat stations reaching 6.4° on one occasion. While differences in minima on opposing slopes did not exceed 2° and were usually 1° or less, even these temperaure differences became critical when they occurred in the freezing range.

Duration of freezing temperature at the various stations on a night of continuous record proved to be a more reliable criterion of relative frost hazard than the minima attained at those stations.

Tomato plants exposed at 14 stations in the valley were killed by freezing at four different dates which ranged from four days before to sixteen days after the official U. S. Weather Bureau "date of first killing frost," indicating at least 20 days difference in length of the fall portion of the potential growing season among the plant habitats in a relatively small topographic unit.

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MOLLUSKS OF SODON LAKE, OAKLAND COUNTY, MICHIGAN. I. STRATIGRAPHIC OCCURRENCE OF SHELLS IN PEAT AND MARL SEDIMENTS

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In connection with palynological studies of Sodon Lake sediments (Cain, '48; Cain and Cain, '48; Cain and Slater, '48a) it was noticed that samples often included numerous shells of small mollusks. Since the Cranbrook group is interested in several aspects of the present and past biological features of this small glacial lake basin, it was decided to resample the sediments for the purpose of ascertaining whether any correlation could be discerned between the occurrence of mollusks and the past history of the lake basin as indicated by pollen analysis.

The samples were obtained at foot-level intervals, by means of a peat-sampling tool, in the same location as those used for pollen work (Cain and Slater, '48a). In several instances additional samples were taken between the foot-level intervals. Altogether the shells were washed from 38 samples of 30 cc. volume each, scattered through a 25-ft. section. Thin layers of clay and sand mark the bottom of the section (over the glacial gravels), but the principal sediment is marl which extends upward to the 8-ft. level with only minor peaty-marl layers interspersed at the 21-ft. and the 14–15-ft. levels. From the 8-ft. level upward the sediments are composed of fen peat with no evidence that either *Sphagnum* or ericaceous plants have ever played at any time a predominant role in the vegetation of the basin. Changes in the character of the sediments are not reflected strongly in the mollusks. The number of shells drops in the peaty layer at 21 ft. It is also relatively low at 15 ft., but it rises rapidly in the upper layers of this zone to a considerable number at 14 ft. The shells are predominantly of aquatic species. Shells of terrestrial species, however, are also present in small numbers in the water-deposited marl. Their numbers are, naturally, somewhat greater in the peat-forming period when the local vegetation was of the fen type (Cain and Slater, '48b).

Table I gives the number of shells of each species. None was recovered from the clay (rock flour) sample at the bottom of the section at 24 ft. 10 in., whereas 18 shells of 4 species were taken from the sandy layers immediately above. With the commencement of marl sedimentation, the variety of aquatic forms increased rapidly at first: 6 at 24 ft., 8 at 23 ft. 9 in., 12 at 23 ft. 2 in., 15 at 22 ft. 6 in., 16 at 21 ft. 10 in. Only three additional species were added later, making a total of 19 aquatic species and varieties. The inwash of terrestrial forms was first encountered at the 19-ft. level, with 5 species. Five more species were added from there up to the 10-ft. level, and 4 more species after fen conditions had developed. The total molluscan fauna removed from comparatively small samples of this section is, then, 33 forms, all of specific rank except for 4 varieties of *Valvata tricarinata* and *Carychium exile* var. *canadense*.[1] This is a moderately rich fauna, the majority of the forms of which entered the waters of Sodon Lake comparatively rapidly in early post-glacial time.

The number of different entities in any one sample ranged from 0 to 20; the average was about 10. The maximum

[1] The names of mollusks follow Baker ('28) for aquatic species and Pilsbry ('39–'48) for land species. We wish to extend our appreciation to C. Bruce Lee, the University of Michigan, for checking our initial determinations and for providing certain critical identifications, and to Henry van der Schalie, Curator of Mollusks, University of Michigan Museums, for encouragement and helpful suggestions.

TABLE I. *The occurrence of mollusks in sediments at Sodon Lake, based on 30 cc. samples*

Depth of sample		Aquatic gastropoda																Sphaeriidae			Terrestrial mollusks														Number of aquatic snails and finger-nail clams	Number of terrestrial forms	Total number of identifiable shells at each level	Increase in variety of aquatic forms, with time	Increase in variety of terrestrial forms, with time
		*Fossaria obrussa	*Fossaria modicella	*Helisoma trivolvis	*Helisoma antrosa	*Helisoma campanulata	*Gyraulus parvus	*Gyraulus deflectus	*Menetus exacuous	*Physella integra	*Valvata tricarinata var. *tricarinata*	*Valvata tricarinata var. *perconfusa*	*Valvata tricarinata var. *unicarinata*	*Valvata tricarinata var. *simplex*	*Valvata sincera*	*Amnicola limosa*	*Amnicola lustrica	*Sphaerium	*Musculium	*Pisidium	*Strobilops labyrinthica	*Vertigo ventricosa	*Vertigo milium	*Retinella indentata	*Retinella electrina	*Helicodiscus parallelus	*Gastrocopta contracta	*Euconulus fulvus	*Zonitoides arboreus	*Oxyloma retusa	*Carychium exiguum	*Carychium exile	*Carychium exile var. *canadense*	*Discus cronkhitei*					
ft.	*in.*																																					
1	0				2							1				1		1														2			4	3	7	19	14
2	0		2						1							2					1													6	3	9		
3	0		10		9		11	17		1	4	5				21	7				4	5		5	2	2			2	42	2		85	63	149		
4	0	1	6		10		15	9	5	6	22	18			1	51	24	5	1	4								2					178	2	180		
5	0		3		2		8	3				2		3		26	9														2			56	2	58		
6	0		8		1		13	6		1		6		2		24	4	4		1	3	4				3					8	1		70	19	89		14
7	0	8			8		18	3	1	3		3		6		18	1	2			6		1	2					1	1	7			71	18	89		13
8	0				8		10	5		2		8	3	5		17															1	1		58	2	60		11
9	0	4	16		28		43	15	5	11		17		28		45	9	4	1		2	3		2		1			2	8		15		226	33	259	19	
10	0		3		4		5	8		6		6		5		19	3											1	1					59	3	62		10
11	0	11	1		10		35	11		6		27		6	1	38	4				2	1							2		3			150	8	158		
12	6		1		39	1	33	9		8		16	2	27		57	11	3																207	0	207		
13	0		1	1	28	1	14	7		7		6		4		60	5																	134	0	134	18	
13	6				16		9			5		11	3	11	1	35		7																98	0	98		
14	0	6	2		31		50	7	2	12		14	4	27		55	2	25		1	1						1		1		2			238	6	244		9
14	6				18		22	9		1	2	25	7	17	2	30															1			133	1	134		
15	0				1		11					3		3	2	13						1									2			33	2	35		7
16	0	1			12		12	11		2		26	15	9	5	47	3																	143	0	143		
17	0		1		8		34	6		1		43	15	13		104	17								1									242	1	243		
17	3	2			8		23	7	3	7		9	5	20	1								1						1					85	2	87		6
18	0	6	4		13		35	5	1	3			15	49		19	1														1			151	1	152		
19	0		1		2		7		2	3		8		3	4	14						1			1		1		2		1			44	6	50	17	5
20	0				10		26	2		4	17	20			1	14																		94	0	94		0
21	0				1		2				4	2			1																				10	0	10		
21	6				1		14			1	4	7	1	1	7	6		3		2															47	0	47		
21	8	2	3		3		25	8			6	25	2		28	5																		107	0	107		
21	10		1		2		31	15		1	21	12			32	18																		133	0	133	16	
22	0						12	2			12	20	2	2	89	7																		146	0	146		
22	6						26	10			19	17			27	8																		107	0	107	15	
23	0			1	3		7	5			10	3			7	7		2		2														47	0	47	13	
23	2				3		10	4			12	4			2	5	1	5		1														47	0	47	12	
23	6						3	5			12					6																		26	0	26		
23	9	1	1		4		5	3			7					4																		25	0	25	8	
24	0				2		9	1			4	1				2																		19	0	19	6	
24	1				4		1				5																							10	0	10		
24	4				3		1				3					1																		8	0	8	4	
Totals																																			3297	175	3472		

* Species known to live in the lake today.

richness occurred at the 9-ft. level, although 19 forms occurred much earlier, at the 14-ft. level. Fewer than 5 species per sample were encountered only at the top (1 ft.) and the bottom (23 ft. 6 in. to 24 ft. 10 in.) except for the anomalous sample at 12 ft., which was unaccountably barren.

The number of identifiable shells from the different 30 cc. samples ranged from 0 to a maximum of 259 at the 9-ft. level, with an average of about 91 shells per sample. There were 4 levels with more than 200 shells, and 11 additional samples with from 100 to 200 shells which were well-scattered through the section.

The species of table I which are known to live in the lake today are indicated by an asterisk before the name. The marsh and terrestrial vegetation of the lake basin has not been searched for mollusks, but numerous samples of the *Chara* mat (Cain, Segadas-Vianna, and Bunt, '50) have revealed the typical aquatic fauna, the *Chara* being nearly the exclusive community of the lake (Cain and Slater, '48b). All the aquatic species known from the sediments have been found living in the *Chara* community of the lake except for *Valvata sincera.* Species not found in the sediments, but found living in the lake or on the shore, include *Physella sayii, Pseudosuccinea columella, Gyraulus hirsutus, Planorbula armigera, Zonitoides nitidus, Stenotrema* (*Polygyra*) *monodon,* and *Mesodon* (*Polygyra*) *thyroidus.* None of the species of mussels of southeastern Michigan has been found at Sodon Lake, either fossil or living.

The percentage composition of the various species, based on total identifiable shells from each sample, was examined for trends and correlations with the findings of pollen analysis with no results of interest except in the case of *Valvata.* This largely negative result may be due partly to the small size of the samples and their wide spacing, but, as already indicated, the percentages are based on an average of about 90 shells per sample.

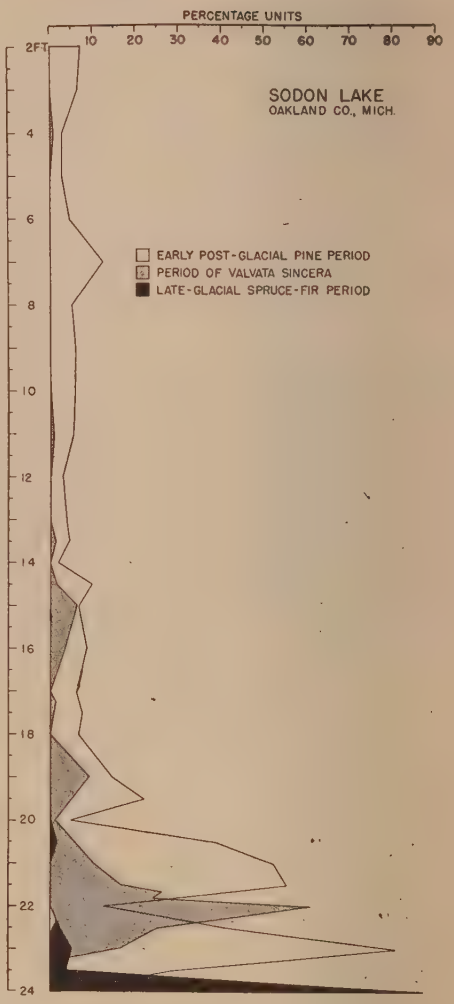

FIG. 1.

Also, even when the samples were taken at closer intervals than 1 ft., the percentages often changed abruptly and somewhat erratically.

The case of *Valvata sincera* provides the strongest correlation between mollusk occurrence and the history of the region as shown by pollen analysis. Figure 1 shows the late-glacial period in which the pollen spectrum was dominated by spruce (with some fir) at the time sedimentation commenced in Sodon Lake. This record, incidentally, is undoubtedly seriously

truncated at the base with the length of the spruce period under-represented—possibly because of the slow melting-out of the ice block that accounts for the origin of the depression. The late-glacial spruce period was followed immediately by the boreal or early post-glacial period of pine dominance in the pollen spectra (see also Cain and Cain, '48, for suggestions as to the rôles played by the species of pine). Pine is present at the beginning of sedimentation, but in small amount, and increases rapidly to a maximum of 80.7% at the 23-ft. level. There is a puzzling decline of pine at the 22-ft. level (with a corresponding increase, principally of oaks) after which the pine increases to 55.2% at the 21.5-ft. level, only to decline rather steadily to an unimportant level from about 18 ft. upward. The decline in pine between the two peaks may represent an oscillation in the position of the ice front—a temporary amelioration of the climate.

Valvata sincera appears at 23 ft. 2 in. and builds up to a maximum of 61% at the 22-ft. level in the middle of the pine period, just when the pine is temporarily low. The percentage abundance of the snail declines in advance of the decline of pine, reaching a low point, as does the pine, at the 20-ft. level. Thereafter it occurs only as an insignificant element in the fauna, but with some very interesting and close correlations with the behavior of pine between the 20- and the 10-ft. levels. *Valvata sincera* in Michigan today is a northern species probably more characteristic of the Lake Forest region than of the forest types prevalent to the south, but it has been collected in 21 counties ranging from the southern counties to those bordering Lake Superior.[2] The Lake Forest region in Michigan commences about 100 miles north of Sodon Lake and is an area of northern hardwood climax (sugar maple and beech) with pines as very important, long-enduring subclimax stages. This is the natural area of the once important Great Lakes pine lumber industry which was largely based on white (*Pinus Strobus*) and red (*P. resinosa*) pine. It is also the area of jack pine (*P. Banksiana*). *Valvata sincera* is typical of the non-acid lakes of the region as it is also of the more northern hardwood-spruce transition zone. The conclusion seems justified that the history of occurrence of *V. sincera* at Sodon Lake is a partial confirmation of the vegetational and climatic history of the area as previously understood from the results of pollen analysis, especially with respect to the early post-glacial pine period.

The results on the occurrence of varieties of *Valvata tricarinata* are likewise of some interest. Figure 2 shows the varietal composition of the species from sample to sample in the section. *V. t. tricarinata* is a little shell with the 3 carinae (ridges) of the body whorl strongly developed. Var. *perconfusa* has the middle carina suppressed; var. *unicarinata* has the middle and lower carinae suppressed, var. *simplex* has all the carinae suppressed. These are true varieties in the sense that all degrees of variation can be found between absence and strong development of the carinae.

Actual percentages are not to be interpreted as exact, for some shells had to be assigned rather arbitrarily to one or another named entity, but since a total of about 850 shells of the species were classified, it is not likely that the principal relationships are far wrong. Var. *tricarinata* predominated in the late-glacial and early post-glacial periods, with somewhat violent fluctuations, and disappeared at the 19-ft. level which marks, also, the end of the boreal pine period. It returns in strength at the top of the sedimentary column, from the 5-ft. level upward. This terminal upswing of *V. t. tricarinata* is suggestive of the so-called recent period

[2] The general distribution of *Valvata sincera*, according to Baker ('28), is "Anticosti Island and Maine, west to Wisconsin, S. E. Kewatin and Lake Winnipeg, south to southern Michigan and northern New York. It is a northern species. Not authentically reported from Illinois."

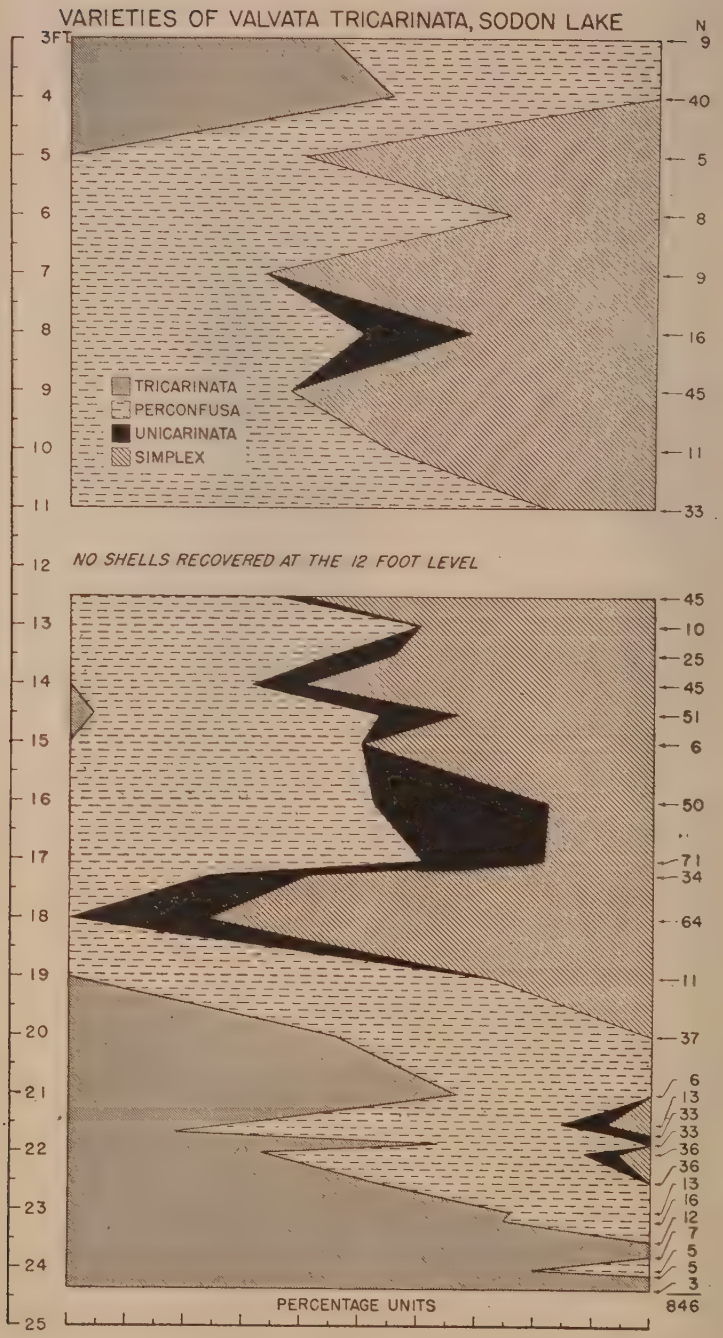
VARIETIES OF VALVATA TRICARINATA, SODON LAKE
N
3FT
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
9
40
5
8
9
16
45
11
33
TRICARINATA
PERCONFUSA
UNICARINATA
SIMPLEX
NO SHELLS RECOVERED AT THE 12 FOOT LEVEL
45
10
25
45
51
6
50
71
34
64
11
37
6
13
33
33
36
36
13
16
12
7
5
5
3
846
PERCENTAGE UNITS

FIG. 2.

of revertence, with cooler and moister climate, but it is not correlated with a similar return to importance of pine pollen, nor do the other results from pollen analysis show much evidence at Sodon Lake or elsewhere in the Central States of a recent "sub-Atlantic" period. Var. *simplex* attains importance only with the onset of the oak period, after the pine period, which it maintains with some fluctuations from the 19- to the 5-ft. level. Its complement during this time is var. *perconfusa* which, however, began to develop importance much earlier, during the pine period. Var. *unicarinata* at no time exceeds 30%, and is usually very much less. We do not find in the literature (Baker, '28) any evidence that the varieties of *Valvata tricarinata* have any known geographic (climatic) or ecological significance. They may have such values, which would be revealed by a closer study.

The variations of *Valvata tricarinata* undoubtedly have a fairly complicated genetic basis. There is little hint that the diagnostic characters for the named varieties are linked with adaptive features. It is entirely possible that the varietal composition of *Valvata tricarinata* may fluctuate widely and in a haphazard or chance manner, even from season to season since the overwintering population is very small. The population begins to build up in the early spring (Cain, Segadas-Vianna, and Bunt, '50) and then suffers depredations by fish and other enemies, a matter, however, about which we have no data. An adequate analysis of the diminished winter population and the greatly enlarged spring population, over a series of years, would probably throw considerable light on this evolutionary question. The results from the sedimentary column appear to reflect some longer-period trends which, for all we know at the present time, may not be adaptive.

Summary

The shells from 30 cc. samples taken at 38 levels in a 25-ft. section of the marl and peat sediments at Sodon Lake were studied as to their vertical distribution and percentage occurrence from late-glacial time (the spruce-fir period) to the present. It was found that the majority of the molluscan fauna, as represented by identifiable shells, appeared in the lake basin in early post-glacial time (the pine period). The total fauna numbers 33 kinds of which 19 are true aquatics. Although the samples studied were rather small (30 cc.) their average identifiable shell content was nearly 100, with a maximum of 259. The richest level in number of species had 20 different forms.

The only obvious correlations between the occurrence of mollusks and the climatic and vegetational history of the area as determined by pollen analysis were found in *Valvata*. *V. sincera,* a comparatively northern species absent from Sodon Lake today, had a period of comparative abundance coincident with the pine period of early post-glacial time. This was likewise true of *V. tricarinata* var. *tricarinata* which, however, also had a final period increase. To the extent of the above cases, the results of pollen analysis and mollusk analysis support one another—a type of investigation worthy of more attention.

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MOLLUSKS OF SODON LAKE, OAKLAND COUNTY, MICHIGAN. II. THE WINTER OCCURRENCE OF CERTAIN SPECIES

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Although the authors of this paper are primarily plant ecologists, they developed an interest in the mollusks of Sodon Lake through efforts to correlate the occurrence of fossil shells in the marl and peat sediments with the late- and post-glacial history of the area as worked out by pollen analysis (Cain, Segadas-Vianna, and Bunt, '50). The above study of the fossil shells was carried out from late fall and winter to early summer and was accompanied by an effort to ascertain the nature of the contemporary molluscan fauna which had not been studied previously.

TABLE I. *Living mollusks washed from* Chara contraria *at about 1 m. water depth, Sodon Lake, Oakland Co., 27 Nov. '48*

Species	Number	Percentage
Amnicola limosa	278	43.1
Valvata tricarinata perconfusa	94	14.6
Amnicola lustrica	85	13.2
Gyraulus hirsutus	54	8.4
Physella integra	49	7.7
Physella sayii	34	5.3
Helisoma campanulata	15	2.3
Menetus exacuous	13	2.0
Helisoma (not identified)	12	1.8
Helisoma trivolvis pilsbryi	5	0.8
Pseudosuccinea columella	4	0.6
Helisoma antrosa	1	0.2
Planorbula armigera	1	0.2
Totals: 13 species	645	

On 27 Nov. '48 we collected a series of shells from the *Chara contraria* mat at about 3-ft. depth of water and made tentative identifications which were kindly verified or corrected by C. Bruce Lee of the University of Michigan. These results, table I, show that *Amnicola* (*limosa* and *lustrica*[1]) composed more than half of the 645 forms of the sample, with *Valvata tricarinata* var. *perconfusa* being of secondary importance. At this season the *Chara* mat had not broken down completely and the lake was not yet covered with ice.

The next effort to study the living mollusks was in February. Various spots in the lake were sampled through the ice by means of a peat-sampling tool, but with no recovery of live mollusks. A search of the literature gave us few hints as to the over-wintering position of the common aquatic species except that they were thought mostly to be buried in the

TABLE II. *Living mollusks from shallow water samples of* Chara *and bottom surface materials, Sodon Lake, Oakland Co., 26 Feb. '49*

Mollusks, 2 qt. samples	Stations			
	1 Nuphar	2 Chara	3 Typha	4 Inlet
Living forms				
Helisoma campanulata	3	2	1	0
Helisoma antrosa	0	1	0	0
Physella integra	0	2	0	0
Amnicola limosa	42	0	1	0
Valvata tricarinata	9	0	0	0
Menetus exacuous	1	0	0	2
Sphaeriidae	0	0	0	23
Totals	55	5	2	25
Empty shells				
Helisoma campanulata	X	X	X	X
Helisoma antrosa	X	X	X	X
Helisoma trivolvis	X	X	X	X
Amnicola limosa	X	X	X	X
Amnicola lustrica	X	X	X	X
Valvata tricarinata	X	X	X	X
Physella integra	X	X	X	X
Physella sayii	X	X	X	—
Menetus exacuous	X	X	X	X
Gyraulus deflectus	X	X	X	X
Fossaria obrussa	X	X	X	X
Pseudosuccinea columella	X	—	—	X
Discus cronkhitei	—	—	—	X
Sphaeriidae	—	X	—	X

Station 1—In the center of a stand of *Nuphar advena;* water 3–4 ft.

Station 2—On the Chara shelf; water about 1–1.5 ft.

Station 3—In the midst of a fragmentary *Typha* stand; water less than 1 ft.

Station 4—Within 6–8 ft. of the mouth of the inlet; no thick ice; no vegetation; bottom of soft mud; water about 1 ft.

[1] The names of mollusks follow Baker ('28) for aquatic species and Pilsbry ('39–'48) for land species.

TABLE III. *Occurrence of living mollusks, Sodon Lake, Oakland County, Michigan, in two-quart samples along radial transects across the Chara shelf from the shore-line outward*

Date	Feb. 28				March 5					April 4						April 26					June 16				
Distance from shore, ft.	18	36	54	72	8	15	22	30	45	1	8	30	48	55	75	5	20	38	45	68	5	17	35	45	53
Water depth, feet	1.6	8.6	16	21	1	3	9	14	22	0.3	0.8	1	3	7	18	0.8	1	1.5	4	13	0.8	1.6	2	8	12
Chara mat (P=present)	P	P	P	—	P	P	P	—	—	P	P	P	P	P	—	P	P	P	P	—	P	P	P	—	—
Bottom temp., ° F.	39	39	40	36	34	40	40	39	39	48	48	49	48	46	41	55	56	54	55	47	69	75	72	70	56
Ice cover																									
Fossaria obrussa	—	—	—	—	—	—	—	—	—	3	—	—	—	—	—	4	—	—	—	—	13	—	—	—	—
Helisoma campanulata	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	1	2	—	—	—	—	—	—	—
H. antrosa	—	—	—	—	—	—	—	—	—	—	—	3	—	—	—	—	—	—	—	—	1	2	10	2	—
Gyraulus parvus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	33	50	2	—	13	—	1	1	—
G. deflectus	—	—	—	—	—	2	—	—	—	9	1	1	—	—	—	2	5	2	—	—	10	26	5	—	1
Menetus exacuous	—	—	—	—	—	1	1	—	—	1	4	—	1	1	—	8	13	15	15	—	—	—	—	—	1
Physella sayii	—	—	—	—	—	—	—	—	—	—	—	3	—	—	—	—	1	1	1	—	6	16	30	8	—
Valvata tricarinata	—	8	2	—	4	15	20	—	—	4	7	1	168	49	—	46	15	12	151	—	1	—	4	30	18
Amnicola limosa	—	8	10	—	—	87	28	—	—	1	1	15	414	82	—	3	13	54	388	—	—	3	22	80	3
A. lustrica	—	—	—	—	—	45	3	—	—	—	2	3	6	—	—	2	3	122	23	—	6	3	8	3	—
Sphaeriidae	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	1	2	—	—	—	—	—	—	—
Total	—	16	12	—	4	152	52	—	—	21	15	27	589	132	—	67	84	258	580	—	65	50	80	125	23
Average per sample for samples containing live mollusks	14.0				69.3					156.8						247.2					68.6				

mud. With this in mind we took foot-level samples of the substratum under the ice and water in three series, two to 4-ft. and one to 7-ft. depths, certainly far below any probable occurrence of wintering snails. Again we were able to recover abundant shells of about 14 species, but no living animals. It was then decided that the peat-sampling tool was inadequate, cutting a core of only about 2-in.

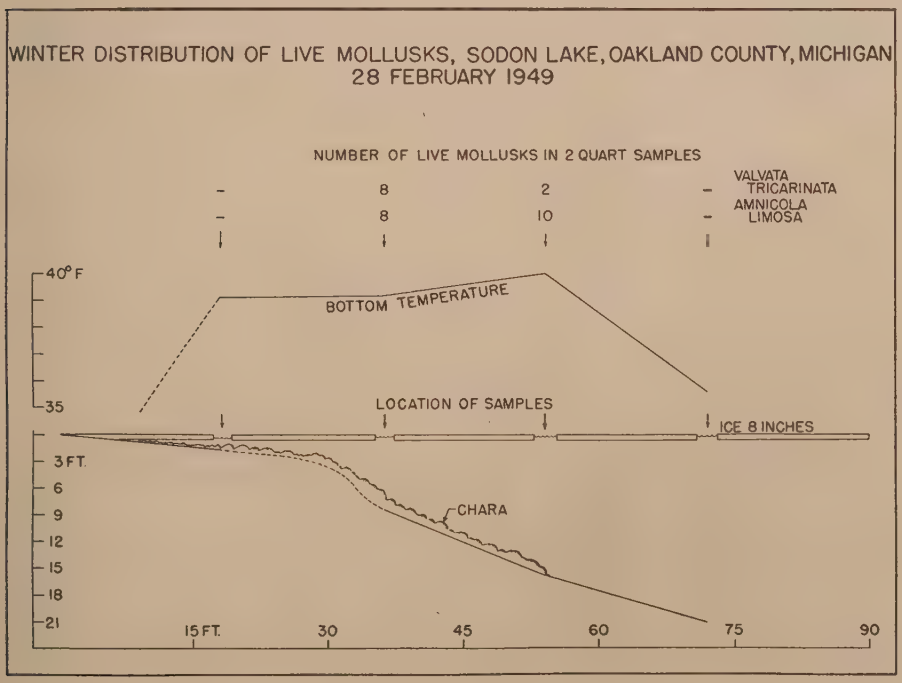

FIG. 1.

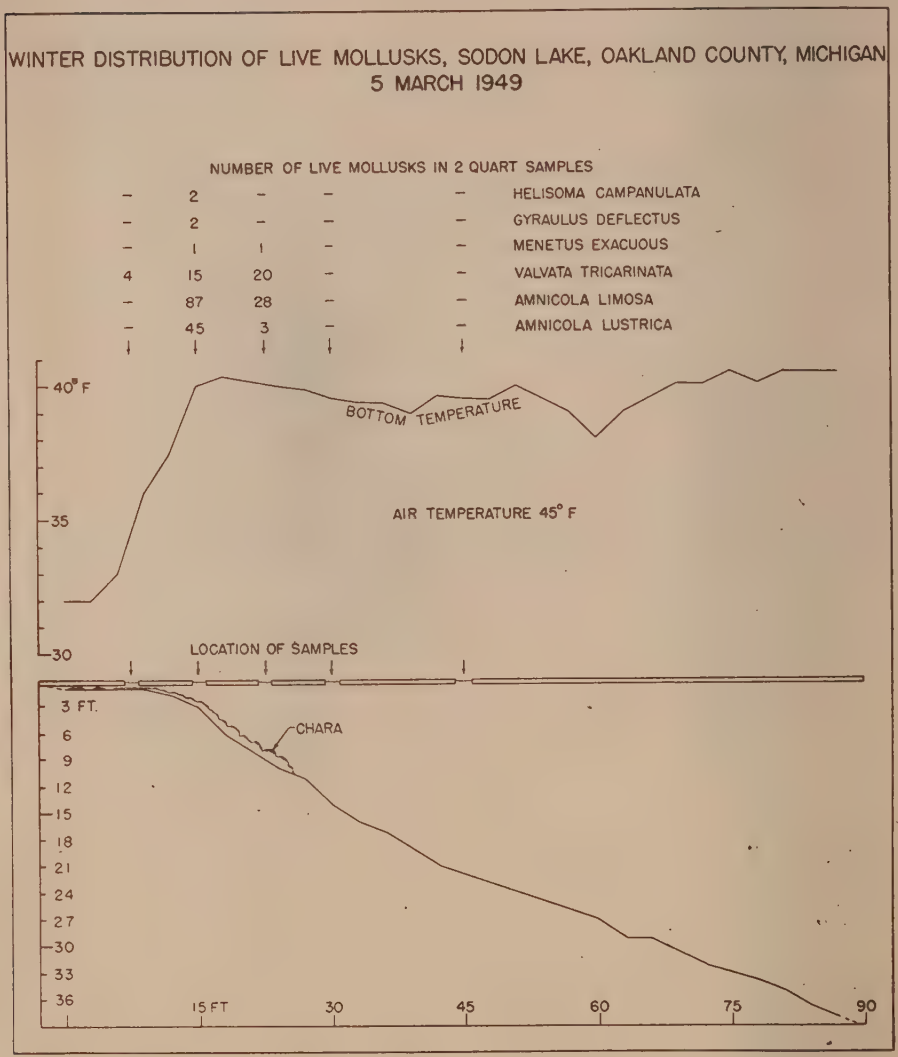

FIG. 2.

diameter, so on 26 Feb. '49 we cut holes about 1 m. square in the ice and sampled the bottom by means of an Ekman dredge. The operation of the dredge in freezing weather was not a simple matter, but the results, table II, included some living mollusks. We then decided to take periodic samples in a regular manner through the remainder of the winter and until the summer population had been established. This investigation is the subject of this paper.

The shallow waters of Sodon Lake, from the shore to depths of about 12 to 16 ft., are occupied principally by a community dominated by *Chara* (Cain and Slater, '48). The bottom of the lake has a form somewhat like a soup plate. There is a gradually sloping shelf of varying width up to 50 or 60 ft. At a water depth

of about 3 ft. this shelf abruptly terminates with a steep slope which in a few feet drops down to 8 or 9 or even 11 to 12 ft. Below this the bottom usually slopes evenly to the maximum depth of about 58 ft. The stature of the *Chara* is adapted to the water depth, being a few inches high in the shallow water and 2 to 3 ft. or more tall at the edge of the shelf and on the slope.

We decided to sample the *Chara* community (ignoring the minor patches of *Nuphar, Nymphaea, Typha,* etc.) at intervals along radial lines from the shore to depths beyond the *Chara* and deeper than the occurrence of live mollusks. The five lines reported on (table III, figs. 1 to 5) were all from approximately the same area of the lake, but no sampling positions were repeated. Each sample was of 2 qts. of material and consisted, in the winter, of the broken-down *Chara* mat together with the surface layers of the substratum. In the seasons when the *Chara* is well developed it was more difficult to obtain bottom material. The samples were lifted by the dredge, or by a bottom scoop where the water was shal-

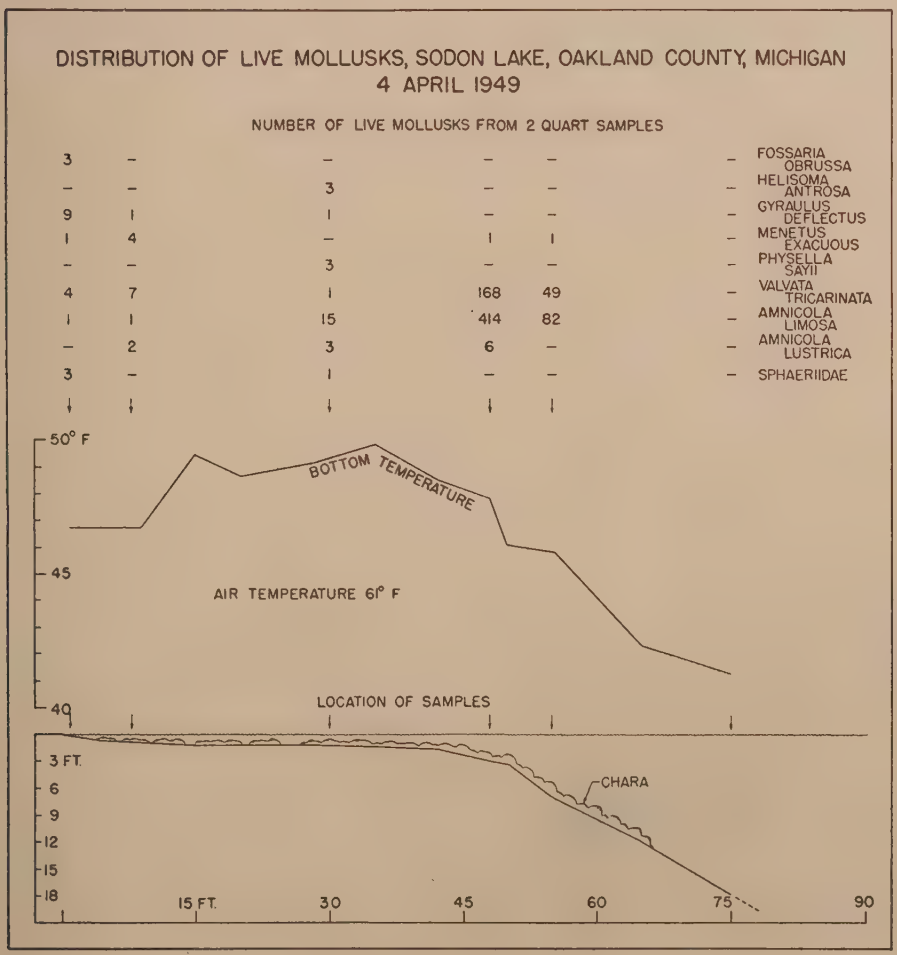

FIG. 3.

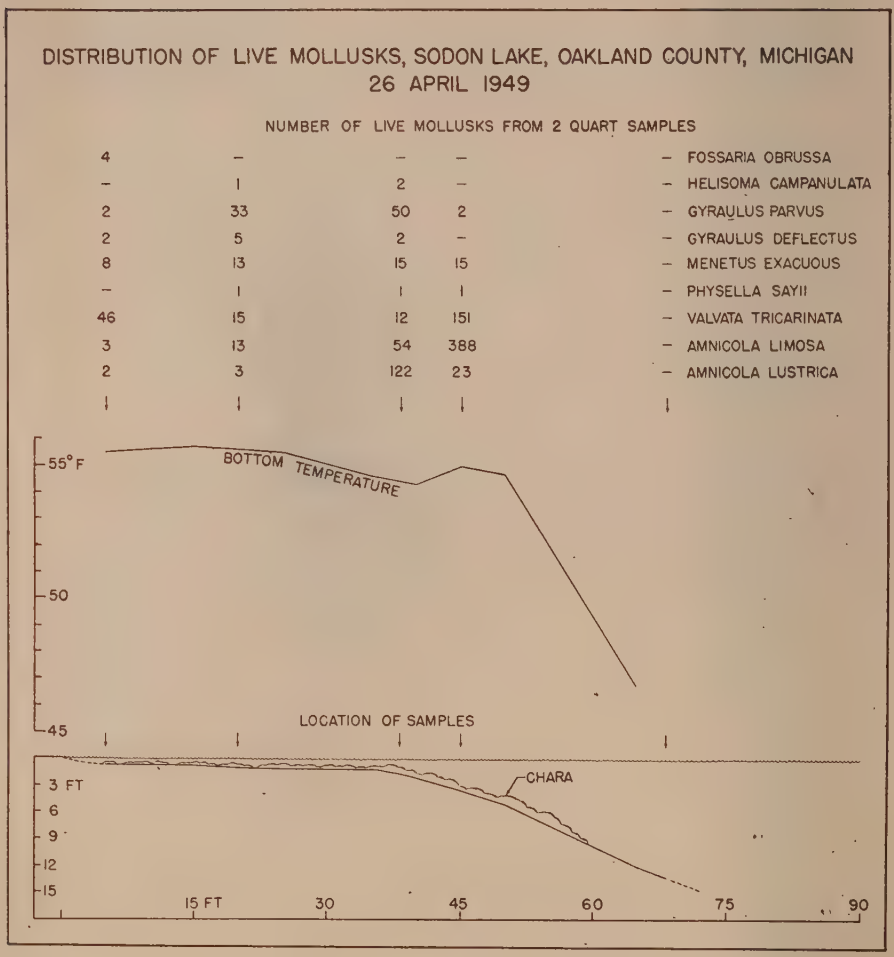

FIG. 4.

low, and dumped into a large flat pan from which a representative 2-qt. sample was bottled. These samples were stored in a refrigerator until studied. The storage, however, was usually only a day or two.

The peaty marl and *Chara* of the samples was washed in a standard sieve set with diameters of 3, 2, 1, and 0.5 mm., respectively, using great quantities of running water. The material held back by each sieve was transferred in small lots to a flat dish, separated in water, and examined under a binocular microscope for living mollusks. The live animals were later sorted by species and counted. The results are shown in table III and figures 1 to 5. Temperatures were taken by means of a Foxboro thermophone which is sensitive to 0.1° F. and comes quickly to a stable reading.

These five sets of data are comparable within the following limitations. Although of the same volume, different samples are qualitatively different. For example, a sample lifted through several feet of water is washed more than one from shallow water. This, we think, is

not an important source of error as the dredge is comparatively large. However, when the *Chara* mat is well developed the dredge jaws do not close completely. What is more critical, possibly, is that the *Chara* and the bottom cannot be sampled equally, at least by our technique, when the *Chara* is of rank growth in the late spring and summer and when the mat is broken down in the winter. It is likely, however, that few live snails are on the bottom under a strongly vegetative *Chara* mat.

The first two series of samples (28 Feb. and 5 March) were taken through the ice, and the subsequent one, 4 April,

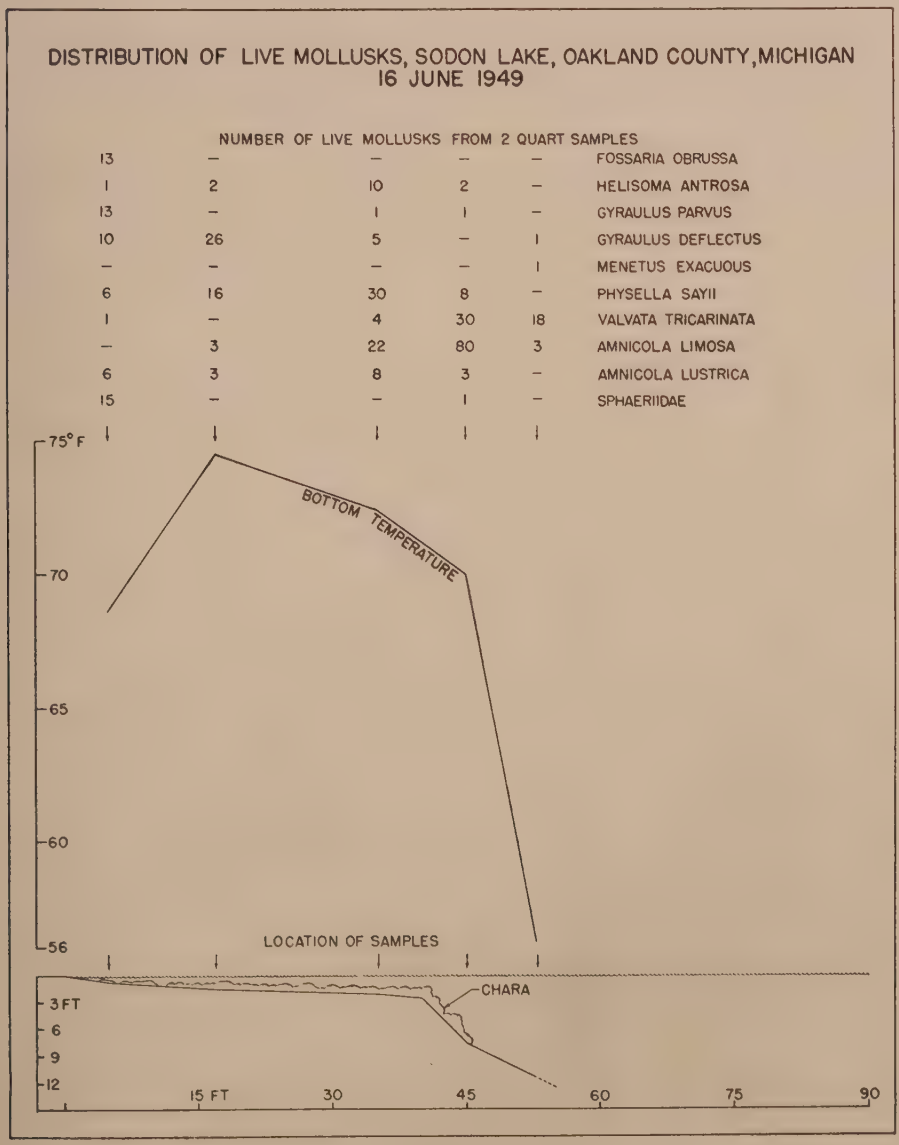

Fig. 5.

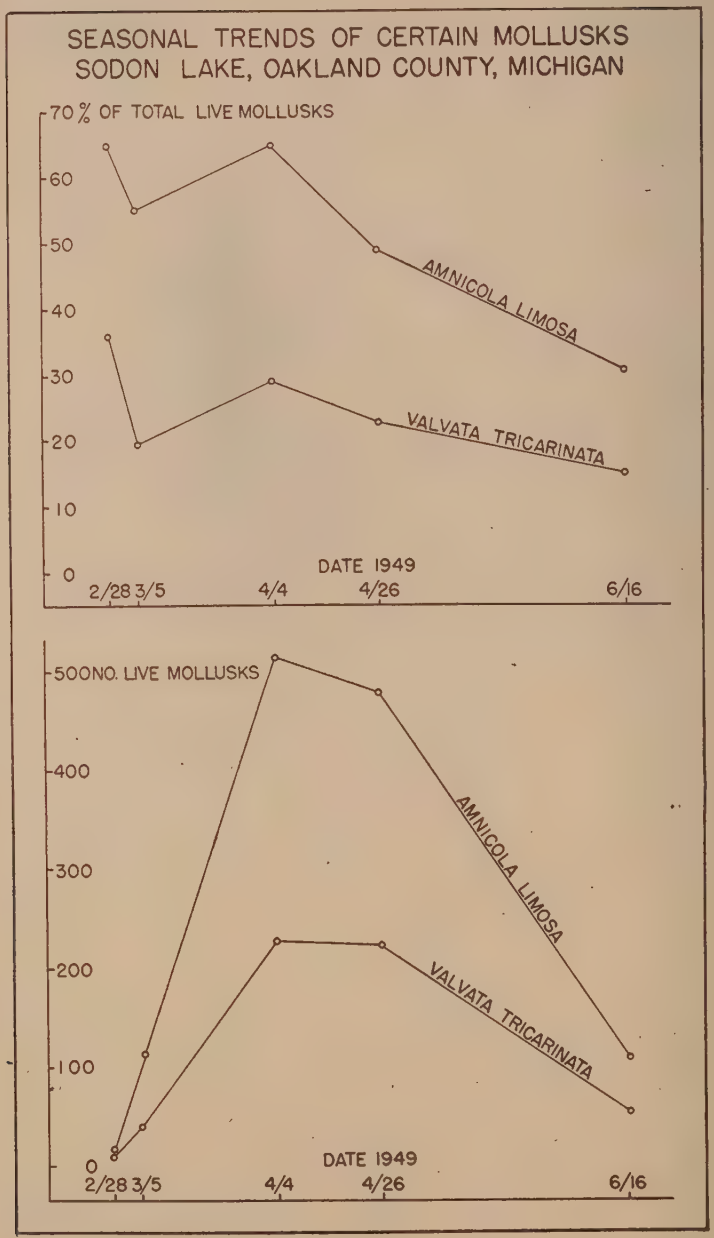
SEASONAL TRENDS OF CERTAIN MOLLUSKS
SODON LAKE, OAKLAND COUNTY, MICHIGAN
70 % OF TOTAL LIVE MOLLUSKS
60
50
40
30
20
10
0
AMNICOLA LIMOSA
VALVATA TRICARINATA
DATE 1949
2/28 3/5
4/4
4/26
6/16
500 NO. LIVE MOLLUSKS
400
300
200
100
0
AMNICOLA LIMOSA
VALVATA TRICARINATA
DATE 1949
2/28 3/5
4/4
4/26
6/16

FIG. 6.

shortly after the ice was off the lake. The total population was very low in February (14 per sample). It began to build up before the ice was off and reached a peak in late April (247 per sample). By June, however, the total population size was reduced, presumably by predation, but this problem has not been studied by us.

The most abundant species at all seasons was *Amnicola limosa*. *Valvata tricarinata* (including its varieties) is of second numerical importance, followed by *Amnicola lustrica*. All these species show the same general pattern of population development, as illustrated in figure 6. Some species never were recovered in quantity. Certain others built up sizable populations (*Gyraulus parvus, Menetus exacuous, Physella sayii*), but much later in the season than *Amnicola* and *Valvata*.

Figures 1 and 2, based on data from 28 Feb. and 5 March, reveal two points about the winter occurrence of mollusks in the situation described: living mollusks do not occur (1) shoreward in any quantity where the temperature of the surface of the bottom is lower than about 40° F.; (2) nor depthward beyond the limits of the *Chara* mat. This latter limit to distribution is likewise true in April (figs. 3 and 4), but by June (fig. 5) some live mollusks were found on the bottom beyond the limits of *Chara*. At all seasons of the year the mollusk population is higher in the deeper water of the shelf and, especially, on the steep slope down from the edge of the shelf where the *Chara* growth is most rank, than at other points sampled.

Our sampling did not encounter certain species which were well known from fossil shells. Of these, *Valvata sincera* has not been taken alive from the lake although it was predominant at one time in early post-glacial time (Cain, Segadas-Vianna, and Bunt, '50). *Fossaria modicella, Helisoma trivolvis,* and *Physella integra* have been taken alive in the lake, but were not found as live forms in the present samples.

Summary

The populations of all the aquatic snails are greatly reduced in size in the winter. The sampling of the present study, however, was inadequate to reveal the overwintering location of some of the less abundant species. In March, while the ice was still on the lake, the snail numbers began to increase. This was especially true of the dominant species *Amnicola limosa* and *Valvata tricarinata*. In the early spring the snail populations began to expand rapidly and toward the close of April most of the species had reached their maximum frequency, although some seem to be later in development. The early summer decline of populations is probably related to predation.

During the winter the mollusks are typically limited to the surface of the bottom: shoreward by temperatures of about 40° F. and depthward by the limits of the *Chara* mat.

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SOME EFFECTS OF WINTER BURNING ON A MODERATELY GRAZED PASTURE

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The grassland formation is one of the most extensive, one of the most varied, and possibly the most valuable, from an agricultural standpoint, of all the climaxes of the North American Continent. As is well known, much of this natural cover of grassland vegetation has been removed by breaking, or has been badly depleted by fire and overgrazing (Weaver '44). That the original prairie was subject to frequent and devastating fires is generally accepted by all grassland investigators. At the Wichita Wildlife Refuge in South Central Oklahoma it was found that the removal of cattle and the subsequent light grazing by the herd of bison greatly increased the fire hazard to the range (Merrill '46). Many investigators have shown that a much greater accumulation of dead plant material occurs in ungrazed, climax patches of prairie than in grazed grassland.

Hopkins, Albertson, and Reigel ('48), in their work on the burning of grassland in Kansas, found that "where litter was heavy at the time of burning, damage was severe and the live cover was reduced by more than one-half" but where the litter was light at the time of burning, the basal cover was reduced very little. They concluded that "the detrimental effect of pasture burning, either accidentally or otherwise, cannot be over-emphasized."

On the other hand, Wahlenberg, Greene and Reed ('39) in their work in the longleaf pine rangelands reported that "annual winter burning maintained more favorable composition, quality, and quantity of forage than did exclusion of fire. The smothering due to pine litter and accumulated dead grass retarded the growth of native grasses and legumes and reduced the number of plants per acre." Cattle on the burned areas gained 37 per cent more than those on unburned pastures. Heyward and Barnette ('34), also working on longleaf pine ranges, showing that "the soils subject to frequent fires were found to be consistently less acid, and to have higher percentages of replaceable calcium and total nitrogen." Campbell and Rhodes ('44) summarized the situation by saying that "controlled burning in the longleaf pine belt . . . can be used when needed to reduce the rough [dead, standing material], avoid the danger of excessive damage from uncontrolled fires, and control brown-spot disease on pine seedlings. There is good experimental and administrative experience to back up the cautious use of prescribed burning in the longleaf-slash pine type."

Aldous ('34), in his work on the effects of burning on Kansas pastures, found that "the plant population was greatest on the plots burned in late fall and least on those burned in late spring. The plots burned in late fall and early spring had a greater number of plants than the unburned plots. . . . Burning stimulated early growth in the spring, owing mainly to higher soil temperatures. . . . Burning did not cause any decrease in the organic matter or total nitrogen over a five-year period." The evidence indicates that "burning seems to be highly desirable if not essential on bluestem pastures about every other year if they are stocked about the same each year."

Curtis and Partch ('50) have shown that the removal of the cover of old litter by fire or clipping brought about a six-fold increase in flower production and a 60 per cent increase in plant height of big bluestem. They also found that "the fertilizing action of the ashes remaining from the burned litter was responsible for a small further increase in flower production but it had no effect on plant height."

Study Area

An opportunity was offered to study the effects of winter burning on a little bluestem (*Andropogon scoparius* Michx.) pasture near Norman, Oklahoma, in the 1949 growing season. Mr. Neil Johnson, who practices conservative grazing on all his land, had noticed that cattle rarely grazed on little bluestem after heavy bunches had been formed. He reasoned that if the tops could be burned off, without burning the mulch and litter on the ground, he would stimulate grazing and obtain more pounds of beef per acre. Accordingly, he burned the large pasture just west of the junction of Oklahoma Highway No. 9 and United States Highway No. 62 in late January, 1949. At the time, the pasture had an uneven cover of snow, remaining from the heavy snowfall of January 18 and lesser snowfalls of January 24 and January 25. Snow to a depth of about five inches remained in the bunches of little bluestem but the surface, in the areas between the clumps, was free of snow. Although burning conditions were fairly favorable, a spotty burn was obtained, with several patches, a half acre or more in area, being untouched by fire. Appropriate studies were made, therefore, on portions burned to the ground level (surface-burned), on parts burned to a height of about five inches (tussock-burned) and on patches untouched by fire (unburned). Our detailed observations began on April 29 and were terminated on August 22, by which time most of the cattle had been removed from the area.

The authors appreciate the interest and cooperation of Mr. Neil R. Johnson, on whose land the study was made, and are indebted to Professors E. O. Hughes, E. L. Rice, and L. M. Rohrbaugh for criticizing the manuscript.

Phenology

Our first observations were made on the burned pasture on March 5, 1949. At that time the unburned patches were brown and the burned area showed black tussocks of little bluestem from 2 to 6 inches in height with interspaces of black residue, reddish soil and an occasional forb seedling (fig. 1). By March 26, little change had occurred in the size of the plants between the clumps and no

Fig. 1. General view of area showing spotty burning, burned patch with blackened tussocks, and unburned tract.

FIG. 2. Burned area (foreground) still showing tussocks on May 21.

growth of grass in the clumps was evident. By April 9, however, the height of the plants in the open had increased by 50 per cent and growth had been initiated in the blackened tussocks of little bluestem. The leaves (1–6 in. high) occurred only on the south (warmer) side of the tussocks and were not evident in, or on the north side of, the tussocks. On April 29, when our first detailed observations were made, the shoots of little bluestem were more numerous and taller on the south side than they were on the north side of the still blackened tussocks. By May 21, the leaves were approximately equal in length throughout the tussocks and had grown almost as long in the unburned clumps (fig. 2).

Vegetative Cover

The average height of the little bluestem in all plots, despite relatively moderate grazing, increased throughout the period of detailed study (April 29 to August 22). Although the stocking was about one head of cattle for each 5.5 acres, the part of the pasture under scrutiny was in excellent range condition. Little bluestem reached average heights of 12 inches, 29 inches, and 52 inches, respectively, in the surface-burned, tussock-burned, and unburned plots. The height of 52 inches in the unburned plots compared favorably with that of little bluestem in a patch of ungrazed prairie nearby.

Average total areal cover was determined at the time of each visit by means of ten temporary quadrats of about one quarter square meter. It will be observed that the areal cover increased in all plots throughout the period of study (table I).

TABLE I. *Increase in areal cover (per cent) during the season in surface-burned, tussock-burned and unburned plots under moderate grazing*

Kind of burn	April 29	May 21	June 23	July 23	Aug. 22
Surface-burned	7	18	33	40	56
Tussock-burned	18	30	55	80	82
Unburned	38	50	74	87	92

The cover on April 29 was mainly due to rough (dead, standing material) and litter (prostrate, weathered, and decaying organic matter) from previous growing seasons. Since much of the rough had been removed from the tussock-burned plots and most of the rough and much

TABLE II. *Oven-dry weight of living and dead material under conditions of moderate grazing in relaiton to burning in a pasture with uneven snow cover (each figure represents an average of two samples only)*

Treatment	April 29	May 21	June 23	July 23	Aug. 22
	Living material, grams per 0.1 square meter				
Surface-burned	0.9	5.5	7.5	11.0	8.5
Tussock-burned	0.5	13.0	16.5	18.0	37.0
Unburned	0.8	15.0	48.0	70.0	151.0
	Dead material, grams per 0.1 square meter				
Surface-burned	18.0	5.0	7.7	7.5	13.0
Tussock-burned	103.0	53.0	47.0	34.0	30.0
Unburned	210.0	135.0	105.0	89.0	—

of the litter had been burned in the surface-burned plots these plots possessed a much lower areal cover than the unburned patches (table I). That all of the plots gained in areal cover throughout the season is not surprising since excellent growth conditions and light grazing prevailed throughout the period of investigation.

The excellent conditions for the accumulation of living plant material are clearly reflected in the data in table II. There was no significant difference in oven-dry weight of living plant material in the three habitats on April 29, but by June 23 it was quite evident that the amount of living material varied inversely with the degree of burning. By the end of the investigation it became evident that there was no significant increase in the accumulation of living plant material in the surface-burned plots. On the other hand moderate increments prevailed in the tussock-burned plots and large gains occurred in the unburned patches (table II).

The amount of dead material was very low in the surface-burned plots at the beginning of our observations and probably did not change significantly during the period of study. It is possible, however, that a greater number of samples might have shown significant differences. In both the tussock-burned and unburned plots the amount of dead plant material decreased throughout the period of investigation, due possibly to the rather rapid decay of litter and the fact that few of the plant parts formed during the growing season died within the period of observation (table II).

At first it was thought that the low production of living material in the surface-burned plots might be due to the relatively poor environmental conditions but we soon found that it was due primarily to the degree of utilization by cattle. Early in the season, especially, it was observed that nearly all the leaves in the surface-burned patches were eaten by cattle (table III). It was noted also that the fresh green leaves on the south side of the blackened tussocks were taken readily by grazing animals. As the grazing season continued the degree of utilization of the surface-burned and tussock-burned areas approached one another. On the other hand, virtually no leaves were grazed in the unburned patches, except in the paths between the bunches of little bluestem (table III). In the period between July 15 and the termination of our observations, cattle were progressively removed from the pasture. Because of this fact, the degree of utilization had become very low on all the plots by the end of the investigation (table III).

TABLE III. *Per cent of leaves grazed in relation to burning in a pasture with uneven snow cover*

Treatment	April 29	May 21	June 23	July 23	Aug. 22
Surface-burned	90	85	50	50	20
Tussock-burned	50	55	35	43	15
*Unburned	1	1	<1	<1	0

* Slight grazing in paths between clumps of little bluestem.

EFFECT OF BURNING ON ENVIRONMENTAL FACTORS

Determinations of light intensity, air and soil temperatures, and soil moisture were made in surface-burned, tussock-

burned, and unburned plots at each visit. In addition, relative humidity was measured in the surface-burned and unburned areas, and wind velocity determinations were made at various levels in an unburned portion of the pasture. All measurements were made between 11 A.M. and 1 P.M. on the study dates indicated. In the interest of brevity, all tabular data on physical factors have been omitted, but may be had upon request.

Light intensity was determined, at a height of three inches, by a Weston illumination meter (number 756) with potential readings up to 10,000 foot candles. Light intensities were determined between 11 A.M. and 1 P.M. on clear days with scattered clouds. The light intensity, above the tops of the grasses, in the unburned area, varied from 9,000 to 10,000 foot candles. In the surface-burned plots the light intensity was fairly constant, with a seasonal average of 5,445 foot candles. The light intensity was considerably lower in the tussock-burned plots (1,330 foot candles) and was rather low in the unburned patches (400 foot candles). Light intensities were still lower (usually less than 100 foot candles) under the lowermost rough and litter.

Air temperatures were taken at a height of three inches above the soil surface with the bulb shaded by a manila card. Soil temperatures were taken at a depth of three inches with an ordinary soil thermometer. Air temperatures were not appreciably different in the surface-burned, tussock-burned, and unburned plots. In several instances the midday temperatures were highest in the unburned patches, presumably due to the lack of movement of heated, trapped air therein. The subsurface soil temperatures were similar in the surface-burned and tussock-burned plots but considerably lower in the unburned station. This was probably due more to the insulating effect of the rough and litter than to that of the living cover.

Percentages of total soil moisture at depths of 0–3 inches and 12–15 inches followed the usual downward seasonal trend for central Oklahoma. The highest soil moisture (21.3 per cent of oven dry weight) was recorded at 0–3 inches in the unburned plot on April 29 and the lowest moisture (4.16 per cent) occurred at 0–3 inches in surface-burned area on July 23. Although the percentages of soil moisture were somewhat more variable in the surface-burned plots, especially at the 0- to 3-inch level, the results suggest that the soil moisture was not appreciably influenced by burning.

As might be anticipated, the per cent relative humidity (at a height of 3 inches) was higher in the unburned area than in the surface-burned plot (55.5 vs. 50.0). This was due, undoubtedly, to the fact that the moist air, caused by transpiration of living plant parts and evaporation from rough, litter, and soil, was not removed by the wind.

Wind velocity in the unburned area was nearly zero at 3 inches above the soil surface and gradually increased upward (in feet per minute) as follows: at 1 ft. = 100, 2 ft. = 220, 3 ft. = 320, 4 ft. = 450, and 5 ft. = 600. Although the 4-foot level was above the tops of the little bluestem, the wind movement was considerably less than at the 5-foot level. Although we used a small vane anemometer (Taylor's Biram Type 3,132) it was not practicable to take readings in or among the tussocks. In the surface-burned area the wind velocity was higher at all levels than it was in the unburned area. At the 5-foot level, in the surface-burned area, it was more than double that at the 3-inch level although no obstructions were present. These facts indicate a considerable reduction in wind velocity near the tops of the grasses due to friction.

Discussion

Several investigators are agreed that burning of pastures through removal of dead grass and litter, stimulates earlier growth of plants in the spring, increases the palatability of grasses (at least for a time) and increases the production of

forbs (including legumes) and annual grasses. They are also agreed that burning decreases the acidity of the soil, increases the percentages of replaceable calcium and total nitrogen and does not alter the amount of organic matter in the soil significantly. Heyward and Barnette ('34) point out that burning does produce a more compact soil, which presumably would erode more rapidly and into which water would infiltrate less readily. In other words, burned-over soils exhibit slightly more favorable chemical characteristics but considerably less favorable physical characteristics than do soils in unburned areas.

It is probable that the harm or good caused by the burning of pastures from the standpoint of soil erosion and plant and beef production, depends primarily on two factors: (1) Whether the rough and litter are destroyed by fire, and (2) whether the perennating parts of the important pasture plants are injured or killed. In some of the investigations the burning was done during dry weather with the result that the dead plant material was largely burned whereas in other studies the burning was done during wet weather in such a manner that much of the lower part of the rough and nearly all the litter were preserved. It is assumed that very little damage to perennating parts can occur when the prostrate dead plant material is not consumed by fire.

In this investigation, much of the lower dead plant material was covered by snow and was, therefore, fully protected from fire. It is possible that a similar result could be accomplished by burning pastures shortly after a heavy rain, when the lower rough and litter were still wet, but when the upper rough was sufficiently dry to burn readily.

Our results suggest that carefully controlled burning during the winter, when two inches or more of snow covered the ground, might make for greater utilization of little bluestem pastures than is at present realized. What is needed is a series of detailed experiments with at least two types of burning and two rates of stocking with cattle. This should be conducted over a three-year period (at least) in order to answer the many questions that have been raised. This can be done well only by an agricultural college or a governmental agency with ample facilities for this type of project. Such an investigation is recommended as a very rewarding one, from the standpoints of both pure and applied science.

Summary

1. A preliminary investigation was made in a pasture near Norman, Oklahoma, concerning the effects of winter-burning on forage utilization and on certain environmental factors.

2. Since burning was done with an uneven snow cover, areas burned to the ground level (surface burned), areas burned to a height of about five inches (tussock burned), and unburned patches were available for study.

3. Burning resulted in earlier growth in the spring, a reduction of areal cover, and a much greater degree of utilization by grazing animals.

4. Burning resulted, also, in increased light intensity, slightly higher midday subsurface soil temperatures, little change in soil moisture, decreased relative humidity, and increased wind velocity.

5. It is suggested that controlled burning in the winter, with at least two inches of snow on the ground, might increase forage utilization in little bluestem pastures, but that more detailed, long-term investigations be conducted before definitive recommendations can be made.

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ASSOCIATIONS BETWEEN FISH SPECIES IN TRIBUTARIES AND SHORE WATERS OF WESTERN LAKE ERIE

CARROLL BLUE NASH

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Often in field collections of fish no attempt is made to retain duplicate specimens taken at the same locality, the purpose being to make a qualitative rather than a quantitative study of distribution. Such was the nature of the collections made in the tributaries and shore waters of western Lake Erie and its islands in June and July of 1948. At each of twenty-nine localities in the area, a sample was taken by minnow seine from the surface to a depth of about four feet in about 75,000 cubic feet of water. The collections were supervised by T. H. Langlois, and species identifications were made by M. B. Trautman and F. C. Daiber.

When collections are taken throughout a sizeable area, several habitats are usually sampled. Each species taken in the collections is associated with each other species to a degree that depends upon the similarity of their habitat preference as well as upon their abundance. Perhaps the best indicator of fish habitat in shallow water is the character of the bottom since, in addition to directly determining the species that inhabit the bottom water, it reflects the rate of flow and the turbidity, factors that affect the species inhabiting the whole depth of the water. It was considered desirable to ascertain the degree of association between the various species taken in the collections with the possibility in view of determining the existence of communities within the area and of correlating these communities with the nature of the bottom.

The twenty-nine localities are divisible on the basis of the nature of their bottoms into three habitats. Listed in the order of the prevailing direction of water flow, they are (1) hard-bottom streams (bedrock, boulders, gravel, sand), (2) mud-bottom waters (mud-bottom streams, drowned river mouths, bays, mud-bottom shores of Lake Erie), and (3) hard-bottom lake shores (sand, gravel and rubble beaches of Lake Erie and its islands). The species taken in more than one collection are arranged in table I according to their primary habitat. For each species is listed the percentage of its total collections that occurred in each of the three regions it inhabited. In computing the percentages, the three habitats are given equal weight by compensating for the inequality of sampling, there being five collections from hard-bottom streams, ten collections from mud-bottom waters and fourteen collections from hard-bottom lake shores.

Locality numbers are listed for each species in table I under the respective habitats in which the localities were situated. The locality numbers refer to the following collection locations. *Hard-bottom streams:* 1. Huron River near Monroeville, bedrock, gravel; 2. Beaver Creek, gravel, sand; 3. Sugar Creek, gravel; 4. Sandusky River near Fremont, bedrock; 5. Portage River below Elmore Dam, sand. *Mud-bottom waters:* 6. Muskellunge Creek, rubble, mud; 7. Rock Creek, mud; 8. South Branch of Muddy Creek, mud; 9. Drainage ditch into Lake Erie, mud; 10. Ten Mile Creek, mud; 11. North shore of East Harbor, mud, vegetation; 12. Sandusky Bay, mud; 13. Portage River at Port Clinton, cinder; 14. Portage River at Port Clinton, mud, vegetation; 15. Lake Erie shore on Long Point, mud, vegetation. *Hard-bottom lake shores:* 16. Entrance to East Harbor, boulders, bedrock; 17. Lake Erie shore at mouth of East Harbor, sand; 18. Kelly's Island, sand, gravel; 19. South Bass Island, sand, gravel, rubble; 20. South Bass Island, sand, gravel; 21. Larcomb's Bay, South Bass Island, sand,

TABLE I. *Arrangement of species in primary-habitat groups, with the percentage of the total collections of each species in each of the three regions it inhabited and the locality numbers in which it was taken*

Species	Hard-bottom streams %	Hard-bottom streams Locality numbers	Mud-bottom waters %	Mud-bottom waters Locality numbers	Hard-bottom lake shores %	Hard-bottom lake shores Locality numbers
Group I, primarily hard-bottom streams						
Campostoma anomalum pullum	100	1-3, 5				
Ericymba buccata	100	1, 2, 5				
Notropis cornutus chrysocephalus	100	1, 2, 4				
Hypentelium nigricans	100	1, 4				
Rhinichthys atratulus meleagris	100	2, 3				
Catonotus flabellaris flabellaris	85	1, 3			15	24
Boleosoma nigrum nigrum	82	1-3, 5	18	7, 12		
Etheostoma blennioides blennioides	81	1, 4, 5			19	22, 24
Micropterus dolomieu dolomieu	81	1, 4, 5			19	19, 24
Semotilus atromaculatus atromaculatus	80	1-4	20	7, 10		
Notropis umbratilis cyanocephalus	75	3-5	25	6, 7		
Pimephales promelas promelas	70	1, 2	30	7, 11		
Ambloplites rupestris rupestris	70	1, 5	17½	13	12½	24
Catostomus commersonnii commersonnii	68	1-5	27	7, 9, 14, 15	5	29
Hadropterus maculatus	67	2	33	7		
Ictalurus lacustris lacustris	67	4	33	13		
Hyborhynchus notatus	54	1-5	38	7-9, 11-14	8	16, 24
Lepomis cyanellus	54	2, 5	46	6, 7, 13, 14		
Notropis spilopterus	49	1, 4, 5	16	12, 14	35	16, 17, 19, 20, 22, 27
Group II, primarily mud-bottom waters						
Ameiurus nebulosus nebulosus			100	8, 9, 15		
Pomoxis annularis			100	6, 8, 12, 14, 15		
Lepisosteus osseus oxyurus			100	13-15		
Lepomis macrochirus macrochirus			100	6, 8, 11		
Notemigonus crysoleucas auratus			100	7, 11, 14, 15		
Carassius auratus			85	8, 9, 12, 15	15	26
Lepibema chrysops			85	8, 9, 12, 14	15	19
Pomoxis nigro-maculatus			85	9, 11, 14, 15	15	16
Dorosoma cepedianum			71	6, 8-10, 12, 14, 15	29	16, 19, 27, 28
Micropterus salmoides			68	6, 11, 15	32	16, 19
Ameiurus melas melas	35	5	65	7-9, 15		
Lepomis gibbosus	39	5	61	6, 11, 13, 14		
Cyprinus carpio	20	2	59	7, 8, 12, 14	11	24
Hybopsis storerianus			58	14	42	26
Perca flavescens			51	9, 14, 15	49	19, 22, 23, 27
Group III, primarily hard-bottom lake shores						
Percopsis omiscomaycus					100	20, 21
Stizostedion canadense canadense			22	14	78	18, 21, 24, 26, 27
Cottogaster copelandi	16	5	11	13	68	16, 18-29
Notropis hudsonius			34	8, 10, 12, 14	66	16-19, 21-23, 26-29
Percina caprodes semifasciata	16	5	25	12, 13, 15	59	16, 18, 20-25, 27, 28
Labidesthes sicculus sicculus			41	11	59	16, 17
Notropis deliciosus stramineus	33	1, 4, 5	11	12, 14	56	16–29
Notropis atherinoides atherinoides	15	1	37	6, 10, 12-14	48	16, 17, 19-22, 24, 26, 28

gravel, rubble; 22. Southwest shore of Middle Bass Island, gravel, rubble; 23. East shore of Middle Bass Island, gravel, rubble; 24. Sugar Island, vegetation, mud, sand, rubble; 25. Big Chick Island, gravel; 26. Fish Point, Pelee Island, sand; 27. North Bay, Pelee Island, rubble; 28. East Sister Island, rubble; 29. North Harbor Island, rubble.

The following species, which were taken in one collection each, are not further considered. Listed with their locality number they are: 1. *Notropis rubellus, Poecilichthys caeruleus;* 3. *Cottus bairdii bairdii;* 4. *Rhinichthys cataractae cataractae, Schilbeodes miurus;* 5. *Moxostoma aureolum, Notropis volucellus volucellus, Noturus flavus;* 6. *Carpiodes cyprinus;* 12. *Hiodon tergisus;* 13. *Boleosoma nigrum eulepis;* 15. *Schilbeodes mollis.*

It can be seen from table I that the species are divisible into three primary-habitat groups. A representative species of each of the groups is listed as follows. *Campostoma anomalum pullum* was found only in hard-bottom streams and occurred in 80 per cent of the collections from this habitat. *Dorosoma cepedianum* was the

TABLE II. *Arrangement of a 2 by 2 table for determining interspecific association*

	Species B		
	Present	Absent	
Species A			
No. of times present	a	b	$a+b$
No. of times absent	c	d	$c+d$
	$a+c$	$b+d$	$a+b+c+d=n$

most widely distributed species in mud-bottom waters, occurring in 70 per cent of the collections from this habitat, but also occurred in 29 per cent of the collections from hard-bottom lake shores. *Notropis deliciosus stramineus* was the most widely distributed species in hard-bottom lake shores and was also the most widely distributed species in the area as a whole, occurring in 100 per cent of the collections from hard-bottom lake shores, 20 per cent of the collections from mud-bottom waters and 60 per cent of the collections from hard-bottom streams.

The degree of association between two species may be measured by any of several coefficients of association. These have been critically reviewed by Cole ('49). In order to determine the degree of association between two species, the data concerning their distribution may be conveniently expressed in the 2 by 2 table shown in table II, A being the less abundant species and B the more abundant species.

With the notation of table II, Cole ('49) derived the following formula for the expression of interspecific association when a positive association exists:

$$C = \frac{ad - bc}{(a + b)(b + d)}.$$

Forbes ('25) previously proposed this formula as a modification of his earlier coefficient of association ('07).

For reasons set forth below, the writer believes that the *phi* coefficient is preferable to the Forbes-Cole coefficient as a measure of the degree of interspecific association. With the notation of table II, the formula for the *phi* coefficient is:

$$phi = \frac{ad - bc}{(a + b)(a + c)(b + d)(c + d)}.$$

The *phi* coefficient apparently originated with Karl Pearson, although it has subsequently been rediscovered by other investigators.

Cole's criticism of the *phi* coefficient is that in order for it to give an association value of $+1$ it is necessary for $a = d = n/2$ and $b = c = 0$. Contrary to Cole, however, it is not necessary for $a = d = n/2$ in order for the *phi* coefficient to show a perfect positive association. Thus, in the following hypothetical table, where the condition $a = d = n/2$ does not exist, $phi = +1$:

		Species B		
		Present	Absent	
Species A	present	100	0	100
	absent	0	50	50
		100	50	150

It is true that for the *phi* coefficient to show a perfect positive association it is necessary for $b = c = 0$. Cole exemplifies his criticism of this characteristic of the *phi* coefficient in the following words: "A parasitic species showing absolute host specificity would not be perfectly associated with the host species if any hosts escaped parasitization." Cole is perfectly correct that the *phi* coefficient is not a proper index of host specificity, but the degree of specificity of the less abundant species (the parasite) to the more abundant species (the host) is not a measure of the entire association existing between the two species. A coefficient of interspecific association should give expression to the degree of association of each of the two species with the other.

Some misleading association values are obtained in the present study with the use of the Forbes-Cole coefficient. For

example, his coefficient indicates a perfect positive association between *Notropis deliciosus stramineus* and *Hypentelium nigricans,* although the latter species was found in only two of the 19 collections containing the former; while, between *Notropis deliciosus stramineus* and *Cottogaster copelandi,* it yields the much smaller association value of + 0.87, although, in this case, the latter species occurred in 14 of the 19 collections containing the more abundant species. Certainly *Notropis deliciosus stramineus* is more closely associated with *Cottogaster copelandi* than it is with *Hypentelium nigricans.*

It can be seen by an inspection of the Forbes-Cole coefficient that it gives less weight to variations of *c* (occurrences of the more abundant species in the absence of the less abundant species) than it gives to variations of *b* (occurrences of the less abundant species in the absence of the more abundant species). On the other hand, the *phi* coefficient gives equal weight to variations of *c* and to variations of *b,* and, indeed, with this coefficient it is not necessary to determine which is the more abundant species in applying the numerical values in the 2 by 2 table. Furthermore, the Forbes-Cole coefficient does not respond to variations of either *c* or *b* when the other factor is *0.*

A coefficient of interspecific association should give equal expression to the degree to which the less abundant species is associated with the more abundant species and to the degree to which the more abundant species is associated with the less abundant species. Also it should be sensitive to variations of the degree to which the more abundant species is accompanied by the less abundant species even where no sole occurrences of the less abundant species are found. Both of these requirements are obtained with the *phi* coefficient, while neither is met by the Forbes-Cole coefficient. For a perfect positive association to be indicated, it is not expected that the less abundant species approach the more abundant species in frequency of occurrence in nature, but that there be no absences of either of the two species in samples containing the other. Thus, the expression of a perfect positive association with the *phi* coefficient is dependent upon the size of the individual samples, but this is also the case when the degree of association is measured by the Forbes-Cole coefficient.

An additional advantage of the *phi* coefficient is that besides serving as a coefficient of association it is also the coefficient of correlation where, as in the present study, the appropriate measure of a species in a collection is simply in terms of presence or absence.

When the species are arranged according to similarity of association as measured by the *phi* coefficient, they separate into three communities (table III). The name of each species, which is listed in the first column of the table, is followed in order by the names of the three species with which it has the highest association values, and, following the name of each associated species, is given the association value between it and the species listed in the first column. When one of the associated species belongs to a different community than the species with which it is associated in the above manner, the number of its community is recorded after its name. The species are arranged in each community in the order of their average coefficient of association with their three most closely associated species of that community. Following the name of each species in the first column is listed the percentage of its total collections which occurred in its primary habitat.

It can be seen that the three communities in table III correspond identically to the three primary-habitat groups in table I, with the exception of *Labidesthes sicculus sicculus.* This species had a slightly higher occurrence in hard-bottom lake shores than in mud-bottom waters (table I), but its closest associations are with species primarily inhabiting the latter region. By the use of the *phi* coefficient, it is shown that the fish species in the shallow waters of the western basin of Lake

TABLE III. *Arrangement of species in communities based on similarity of association; coefficients of association between each species and its three most closely associated species*

Species and percentage occurrence in primary habitat	Associated species and coefficients of association		
Community I, Primarily hard-bottom streams			
Campostoma anomalum pullum, 100	*E. buccata* .85	*B. n. nigrum* .78	*R. a. meleagris* .68
Ericymba buccata, 100	*C. a. pullum* .85	*B. n. nigrum* .67	*N. c. chrysocephalus* .63
Notropis cornutus chrysocephalus, 100	*H. nigricans* .80	*S. a. atromaculatus* .67	*E. buccata* .63
Boleosoma nigrum nigrum, 82	*C. a. pullum* .78	*E. buccata* .67	*S. a. atromaculatus* .57
Hypentelium nigricans, 100	*N. c. chrysocephalus* .80	*E. b. blennioides* .60	*M. d. dolomieu* .60
Etheostoma blennioides blennioides, 81	*M. d. dolomieu* .76	*A. r. rupestris* .61	*H. nigricans* .60
Micropterus dolomieu dolomieu, 81	*E. b. blennioides* .76	*A. r. rupestris* .61	*H. nigricans* .60
Semotilus atromaculatus atromaculatus, 80	*N. c. chrysocephalus* .67	*B. n. nigrum* .57	*P. p. promelas* .54
Pimephales promelas promelas, 70	*H. maculatus* .68	*B. n. nigrum* .54	*S. a. atromaculatus* .54
Ambloplites rupestris rupestris, 70	*E. b. blennioides* .61	*M. d. dolomieu* .61	*E. buccata* .52
Hadropterus maculatus, 67	*P. p. promelas* .68	*B. n. nigrum* .53	*L. cyanellus* .53
Rhinichthys atratulus meleagris, 100	*C. a. pullum* .68	*B. n. nigrum* .53	*S. a. atromaculatus* .53
Catostomus commersonnii commersonnii, 68	*C. a. pullum* .55	*B. n. nigrum* .52	*S. a. atromaculatus* .52
Catonotus flabellaris flabellaris, 85	*C. a. pullum* .52	*A. r. rupestris* .52	*H. notatus* .35
Notropis umbratilis cyanocephalus, 75	*B. n. nigrum* .44	*S. a. atromaculatus* .44	*L. cyanellus* .44
Hyborhynchus notatus, 54	*B. n. nigrum* .53	*C. carpio*—II .53	*C. c. commersonnii* .46
Lepomis cyanellus, 54	*L. gibbosus*—II .67	*H. maculatus* .53	*N. u. cyanocephalus* .44
Ictalurus lacustris lacustris, 67	*H. nigricans* .46	*N. c. chrysocephalus* .35	*L. o. oxyurus*—II .35
Notropis spilopterus, 49	*N. d. stramineus*—III .57	*E. b. blennioides* .40	*M. d. dolomieu*, .40
Community II, Primarily mud-bottom waters			
Ameiurus nebulosus nebulosus, 100	*C. auratus* .74	*A. m. melas* .74	*L. chrysops* .44
Carassius auratus, 85	*A. n. nebulosus* .74	*P. annularis* .52	*L. chrysops* .52
Pomoxis annularis, 100	*D. cepedianum* .58	*C. auratus* .52	*L. chrysops* .52
Lepibema chrysops, 85	*D. cepedianum* .58	*C. auratus* .52	*P. annularis* .52
Pomoxis nigro-maculatus, 85	*N. c. auratus* .61	*M. salmoides* .52	*A. n. nebulosus* .44
Dorosoma cepedianum, 71	*P. annularis* .58	*L. chrysops* .58	*M. salmoides* .40
Micropterus salmoides, 68	*P. nigro-maculatus* .52	*L. m. macrochirus* .44	*L. s. sicculus* .44
Lepisosteus osseus oxyurus, 100	*N. c. auratus* .52	*P. annularis* .44	*P. nigro-maculatus* .44
Lepomis macrochirus macrochirus, 100	*P. annularis* .44	*M. salmoides* .44	*L. gibbosus* .44
Ameiurus melas melas, 65	*A. n. nebulosus* .74	*C. auratus* .52	*C. c. commersonnii*—I .44
Perca flavescens, 51	*D. cepedianum* .39	*L. chrysops* .38	*P. nigro-maculatus* .38
Labidesthes sicculus sicculus, 41	*P. nigro-maculatus* .44	*M. salmoides* .44	*L. m. macrochirus* .26
Notemigonus crysoleucas auratus, 100	*P. nigro-maculatus* .61	*L. o. oxyurus* .52	*P. p. promelas*—I .42
Lepomis gibbosus, 61	*L. cyanellus*—I .67	*L. o. oxyurus* .44	*L. m. macrochirus* .44
Cyprinus carpio, 59	*H. notatus*—I .53	*P. annularis* .44	*L. chrysops* .44
Hybopsis storerianus, 58	*S. c. canadense*—III .53	*L. o. oxyurus* .35	*N. c. auratus*. 29
Community III, Primarily hard-bottom lake shores			
Cottogaster copelandi, 68	*P. c. semifasciata* .66	*N. d. stramineus* .61	*S. c. canadense* .32
Percina caprodes semifasciata, 59	*C. copelandi* .66	*N. d. stramineus* .41	*N. atherinoides* .26
Notropis hudsonius, 66	*N. d. stramineus* .46	*S. c. canadense* .32	*C. copelandi* .31
Notropis deliciosus stramineus, 56	*N. spilopterus*—I .57	*C. copelandi* .61	*N. hudsonius* .46
Percopsis omiscomaycus, 100	*P. c. semifasciata* .28	*C. copelandi* .26	*N. atherinoides* .26
Stizostedion canadense canadense, 78	*H. storerianus*—II .53	*C. copelandi* .32	*S. c. canadense* .32
Notropis atherinoides atherinoides, 48	*N. spilopterus*—I .33	*N. d. stramineus* .32	*N. hudsonius* .31

Erie are associated into three communities according to the nature of the bottom of their primary habitat, although many species occur in two and a few in all three habitats (table I).

The highest coefficients of association occurred between the following pairs of species: *Campostoma anomalum pullum* and *Ericymba buccata* .85, *Notropis cornutus chrysocephalus* and *Hypentelium nigricans* .80, *Campostoma anomalum pullum* and *Boleosoma nigrum nigrum* .78, *Etheostoma blennioides blennioides* and *Micropterus dolomieu dolomieu* .76, *Ameiurus nebulosus nebulosus* and *Carassius auratus* .74, and *Ameiurus nebulosus nebulosus* and *Ameiurus melas melas* .74. In general the highest degrees of association occurred between species primarily inhabiting hard-bottom streams and the lowest degrees of association occurred between species primarily inhabiting hard-bottom lake shores. Most of the latter species exhibited close associations also with a member of one of the other two communities.

Species primarily inhabiting waters in the deeper portion of the lake, such as *Stizostedion vitreum vitreum*, *Aplodinotus*

grunniens, Lota lota maculosa and *Ictalurus punctalus,* may constitute a fourth community in the waters of the basin of western Lake Erie. Such species as *Perca flavescens, Hybopsis storerianus, Stizostedion canadense canadense* and *Percopsis omiscomaycus,* which were found in the present study to be associated with shallow forms, may be more closely associated with these deeper water species.

Association values between most species will vary with the season of the year and with the age of this fish as may their primary habitat, the values reported here being for June and July and for fish of sizes collectable by minnow seine. The presence of dominant year classes in some species may cause their association values to vary somewhat from year to year.

Needless to say, the accuracy of the coefficient of interspecific association for a particular region varies directly with the proportion of the region covered by the sampling, and with the uniformity of distribution of the samples throughout the area if the area is not homogeneous with respect to association between the two species.

In determining the degree of association between two species the size of the individual sample is of great importance. Whether or not two species will occur in the same sample obviously depends upon the size of the sample. Increasing the size of the sample up to a certain point will increase the probability of the joint occurrence of the two species in the sample. To illustrate the effect of the size of the individual sample on the association value, if the samples in the present study had been extremely large, many pairs of species would have occurred only jointly and coefficients of + 1 would have occurred between them, whereas, with the sample size of 75,000 cubic feet that was used, no coefficients of + 1 were found. If the samples in the present study had consisted of only a few cubic feet of water, most pairs of species would have exhibited no joint occurrences and negative coefficients would have prevailed. No problem is involved when the size of the sample is established by the nature of the material studied. For example, in a study of the association between mite species parasitic on rats, the mite population of a single rat is a logical sample. But in many cases an arbitrary value must be assigned to the size of the sample. Since the association values are affected by the sample size, the size of the individual sample must be considered in comparing association values, even where the same coefficient of association is used.

In conclusion, the fish species inhabiting the tributaries and shore waters of western Lake Erie and its islands occur in three communities, which are characterized by the type of bottom of the water primarily inhabited. These are the primarily hard-bottom stream community, the primarily mud-bottom water community and the primarily hard-bottom lake-shore community. While many species occur in from two to all three habitats, nearly every species has its highest degrees of association only with species that have a primary habitat preference similar to its own.

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A STUDY OF TWO COMMUNITIES OF THE NEW JERSEY PINE BARRENS AND A COMPARISON OF METHODS [1]

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INTRODUCTION

The plant life of the pine barrens of New Jersey has been an object of scientific interest for many years. Lutz ('34) states concerning the region ". . . indeed, few other areas in North America have attracted such long continued and widespread attention." Stone ('11), in speaking of the area, called it one of the most interesting botanical areas in the United States and one of the most extensive in the middle Atlantic states left in the primeval condition. Even in more recent times, Moore ('39) spoke of the region as "one of the few large wilderness areas remaining in the eastern United States."

The Pine Region occupies approximately 2,000 square miles of the eastern Coastal Plain of New Jersey (Moore '39). The region is of low relief, the soils being sandy except for areas along the streams and the poorly drained depressions. The climate of the central part of this area, where the present study was made, is characterized by an annual precipitation of between 46 and 48 inches, 24 inches of which falls in the period from April through September. The frost-free period is approximately 180 days in length, lasting from around April 25 to October 20 (USDA Yearbook '41).

The vegetation of the upland parts of this area is characterized by forests of pine and oak, with an understory of ericaceous shrubs and scrub oak. These forests are of all ages due to past fires and cutting. Little ('46) states that the majority of the upland sites are occupied by forests of arborescent and scrub oaks mixed with pines.

The ecological aspects of the upland vegetation have been studied by both botanists and foresters. Harshberger ('16) published a lengthy ecological study of the region, parts of which, in the light of more recent work, appear to be somewhat superficial. Lutz ('34a) made an excellent study of the low sprout growth "plains" vegetation of the region. He attributes this growth form to the frequency of fires on those areas. Little and Moore ('45), Little ('46), Little, Allen and Moore ('48), and Little and Moore ('49) have published a series of studies on the effects of past fires on forest composition and the use of fire as a silvicultural practice in the region.

In spite of the rather voluminous literature on the vegetation of the region, little work has been done in the way of quantitative analysis of the plant communities.

The aim of the present study is to compare the structure of the vegetation of two of the upland forest stands. At the same time, an attempt is made to ascertain the comparability of data obtained by the quadrat method and those obtained by the transect method. The data were obtained in 1948 and 1949 during the months of June and July.

The two areas studied are in the Lebanon State Forest near New Lisbon, New Jersey. The first community is a forest dominated by *Pinus rigida* [2] and containing several species of *Quercus*. It is located on the south side of North Branch Road about one half mile east of where it crosses Middle Branch (39° 55′ N, 74° 29′ W). The second forest community is dominated by *Quercus montana* and *Q. velutina* and contains smaller amounts of *Pinus rigida* and other species of *Quercus*. It is located on the west side of Butler

[1] This study was supported by a grant from the Research Council of Rutgers University.

[2] Nomenclature follows Muenscher ('46) for woody plants, and Robinson and Fernald ('08) for herbaceous species.

Place Road where it crosses the Burlington-Ocean County line (39° 54.5′ N, 74° 26.5′ W). Both communities have heavy shrub layers, but the herbaceous vegetation is very sparse The herb layer was not studied in this investigation.

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Methods

Vegetation analysis

In comparing the structure of the vegetation of the two plant communities, two methods of community analysis were employed, the quadrat method, and the line transect method. In this way, the structure of the vegetation could be more completely studied, and at the same time, it was hoped that an evaluation of the two methods could be made.

Quadrat method.—The size and number of quadrats were the same as have been employed by several investigators in the eastern deciduous forest (Cain '35, Daubenmire '36, Eggler '38, Buell and Wilbur '48, and others). In this study, the arborescent layer was sampled on 10 × 10 meter quadrats established on alternate sides of compass lines. The distance between the quadrats was 10 meters, and between the lines 20 meters. In these quadrats the number of individuals and their diameter at breast height were recorded for all trees over 1 inch dbh. From these data, density (number of individuals per unit area), frequency, and basal area were determined. The shrub and herbaceous layers were not sampled by the quadrat method.

Transect method.—The line transect method, as used by Bauer ('36) and further supported by the same author (Bauer '43), was chosen as the basis for the second method used in studying the woody vegetation in the two communities. The method has also been successfully used by Wells ('46) for a shrub community and by Canfield ('41) for grassland but so far as the authors know it has not been applied to the tree layer, although Gates ('49: 37) indicates its applicability. It consists of laying out a series of line transects and recording the linear distance that each plant spreads over the line. With an adequate sample, the total of this distance for each species is essentially proportional to the cover contributed by that species. By recording the number of individuals of each species that contribute cover on the transects, it is possible to determine the relative numerical abundance of the various species (Bauer '43). Frequency data can be obtained by determining the per cent of the transects on which each species is encountered (Bauer '43). In order to obtain basal area data for comparing with that obtained from the quadrat sampling, the diameter at breast height was taken of all trees over 1 inch dbh that contributed cover on the transect. In addition to measuring the linear distance of cover of the plants, the distance on the transect not covered by any vegetation in each layer was recorded as open space.

The tree layer was sampled on ten 100-meter transects laid out end to end on each of a series of parallel lines established with compass and string. The lines were 20 meters apart. Along the string, a 20-meter tape was suspended horizontally at shoulder height, and the linear distance occupied by each species was recorded in centimeters. Five such 20-meter segments made up each 100-meter tree transect. The shrub layer was sampled on ten 20-meter transects placed directly under the first 20-meter segment of each of the 100-meter tree transects. In this way, each shrub transect could be studied in reference to its particular tree canopy. The tape was placed on the ground for making cover and open space measurements in the shrub layer.

In using the line transect method on the tree layer, a means of getting accurate crown projection on the transect line had to be found. Simple estimation, by eye, of the point where the tree crowns crossed

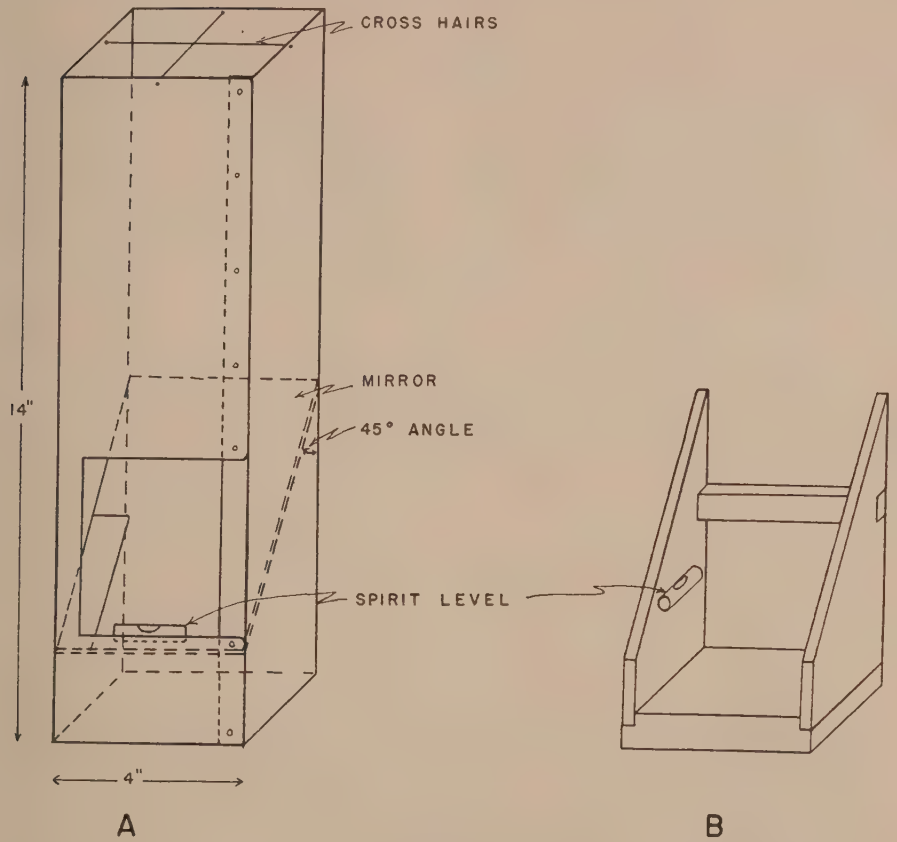

FIG. 1. Diagram of cover sight used in determining limits of tree crowns. A. The instrument from the side that faces the operator, with mirror support removed (see B). B. The support for the mirror. It is attached on the inside at the base of the instrument tube. The spirit level on the side can be seen through the rectangular window scraped in the mirror at its lower left (see A).

the line was both difficult and inaccurate. To overcome this difficulty, a simple cover sight (fig. 1) was designed and built which was found to be quite adequate for the purpose. It consisted of a vertical tube 14 inches long and with a square cross-section 4 inches wide in which a mirror was set at an angle of 45 degrees from the horizontal. A hole was cut in the tube opposite the mirror so that by looking in at the mirror, objects directly overhead could be seen. In order to insure that the sight was held perfectly vertical, two horizontal spirit levels were installed, one parallel to the transect line, the other at 90° to the transect line (fig. 1). Cross hairs were placed on the top of the sight and a cross was made on the center of the mirror. When the two spirit levels were centered, and the cross hairs lined up with the cross on the mirror, accurate crown projection could be made. A few minutes of practice was enough to gain the necessary skill for both rapid and accurate use of this sight. A later improvement of the instrument incorporated, in place of the spirit levels, a plumb bob method of insuring vertical alignment. A heavy sewing needle suspended on a thread from the center of the top opening could then be

lined up with a dot in the center of the mirror. The thread was made long enough so that by tilting the instrument slightly past the vertical the plumb bob could come to rest on the mirror, thus reducing the time necessary for bringing the plumb bob to rest. The tube can be made out of sheet metal, wood, or heavy cardboard. The metal tube has the advantage of being usable in wet weather, without becoming warped.

Age determination

The relative ages of the two communities were determined from increment cores. These were taken with a Swedish increment borer from several trees in each size class.

Light determination

Light measurements were made under the canopy of both communities at the 2 meter level. A Weston sunlight illumination meter (Model 756) with a quartz filter on the photronic cell was employed. One hundred readings were made at 1-meter intervals on lines through the centers of the areas in which the vegetational analyses were made. The light intensity in the open was ascertained before entering each community and again upon completion of the series in the community. The average intensity of these two determinations was taken to be the light intensity value for full sunlight. Light values are expressed as per cent of total sunlight. All light readings were made between 1:30 and 2:30 P.M. standard time. The sky was completely cloudless during the time the readings were made. Readings taken in the open before and after those made in the oak stand were uniformly 10,000 foot candles. Those taken in the open before working in the pine stand were uniformly 9,700 foot candles, while the twenty readings made

FIG. 2. Photograph taken in the pine stand, winter aspect.

following the work in the pine stand averaged 8,050 foot candles ranging from 7,000 to 9,100 foot candles.

Soils

Soil samples were collected from the A and the B horizons in both communities. Mechanical analyses were made using the Bouyoucos hydrometer method (Bouyoucos '36).

Results

The vegetation

The pine stand.—As can be seen from figure 2, the pine stand is a rather open community of coniferous evergreens with which are associated several species of oak. Under this tree canopy is a fairly heavy shrub layer made up primarily of ericaceous shrubs and scrub oaks.

a. *The tree layer.* By far the most important tree species is pitch pine (*Pinus rigida*), contributing, on the basis of the sampling, 70 per cent of the total tree cover, 76 per cent of the total tree density and 82 per cent of the total basal area (table IV). Shortleaf pine (*Pinus echinata*), though much less abundant than *P. rigida,* is, nevertheless, next in importance in basal area, contributing 6 per cent. This species makes up 5 per cent of the total tree density and 7 per cent of the total tree cover. The three most important oaks are the post oak (*Quercus stellata*), the blackjack oak (*Q. marilandica*) and the black oak (*Q. velutina*). There are more individuals of the first two, each comprising 8 per cent of the total tree density, while *Q. velutina* comprises only 2 per cent. In terms of cover and basal area, however, *Q. velutina,* a larger tree, is more important, contributing 14 per cent and 6 per cent, respectively. *Q. stellata* contributes 4 per cent of the total tree cover and 5 per cent of the total basal area. *Q. marilandica* contributes 2 per cent of the total tree cover and only 0.2 per cent of the total basal area. *Sassafras albidum* and white oak (*Quercus alba*) are both present in small numbers.

Table I. *Frequency, density and basal area data from the quadrats, and cover data from the transects for the tree layers in the two stands. Density is expressed in terms of the number of individuals per 2,500 square meters*

Species	Density, frequency and basal area per 2,500 sq m								
	Trees 1 in. dbh and over						Total density	Total basal area in sq ft	Total cm of cover per 1,000 m linear distance
	1–3 in.		4–9 in.		10 in. or over				
	D	%F	D	%F	D	%F			
Pine stand									
Pinus rigida	27	48	48	84	22	72	97	30.5	29,820
Pinus echinata			5	16	1	4	6	2.4	2,860
Quercus marilandica	11	32					11	0.1	875
Quercus stellata	7	8	3	8	1	4	11	2.0	1,640
Quercus velutina					2	8	2	2.1	6,080
Sassafras albidum	1	4					1	.06	360
Quercus alba									960
Oak stand									
Quercus montana	65	64	50	84	4	16	119	17.0	43,750
Quercus velutina	36	44	5	20	12	44	53	13.9	39,870
Pinus rigida	31	52	12	32	8	32	51	10.2	16,660
Quercus marilandica	3	8					3	0.07	
Quercus stellata	6	12	1	4			7	0.3	1,370
Sassafras albidum	1	4					1	0.005	
Quercus alba									200
Pinus echinata									2,030

The discontinuity of the tree canopy can be inferred from the data on total tree cover and open space in table III. The total cover of all tree species is 43 per cent, and the open space in the tree canopy amounts to 58 per cent of the 1,000 meters sampled in the transects.

The distribution of the size classes of the various species can be seen in table I. There is a greater proportion of the individuals of *Pinus rigida* in the larger size classes in the pine stand than in the oak stand. Twenty-three per cent of the total density of this species is represented by individuals of the largest size class (10 inches or over), whereas in the oak stand only sixteen per cent fall into this size class. In the smallest size class (1–3 inch), the opposite is true. In the pine stand it is 28 per cent as compared to 61 per cent in the oak stand. The two dominant oaks in the oak stand (*Quercus montana* and *Q. velutina*) show decreasing density with increasing size.

b. *The shrub and herb layers.* The most important species in the shrub layer are the ericaceous shrubs. Of these, *Gaylussacia baccata* and *Vaccinium vacillans* contribute 29 per cent and 25 per cent of the total shrubby cover respectively (see table II). These shrubs are slightly over one half meter in height. In this same height class are *Gaylussacia frondosa, Ilex glabra, Myrica pennsylvanica, Myrica peregrina, Pieris mariana,* and *Kalmia angustifolia.* Of a somewhat lower height is *Vaccinium angustifolium* which is nearer one half meter in height. Under this layer is a discontinuous layer of *Gaultheria procumbens.* This species is around ten centimeters in height. Its importance in the community can be seen from the data in table II. It contributes 11 per cent of the total shrubby cover and occurred on 70 per cent of the transects.

The scrub oaks, *Quercus ilicifolia* and *Q. prinoides,* together with young saplings of *Q. marilandica* and *Q. stellata,* occur in clumps which tower over the rest of the shrub layer. These clumps

TABLE II. *Per cent of total cover and per cent frequency of the shrubby species in the two stands with the differences calculated. These data are from the ten 20-meter shrub transects in each community*

Species	% of total cover		% frequency	
	Pine stand	Oak stand	Pine stand	Oak stand
Gaylussacia baccata	29	39	100	100
Vaccinium vacillans	25	21	100	100
Quercus ilicifolia	20	1	80	40
Gaultheria procumbens	11	2	70	40
Quercus marilandica	5	0.0	90	0
Quercus prinoides	4	2	40	40
Gaylussacia frondosa	2	28	50	100
Ilex glabra	1	0.4	30	40
Pinus rigida	0.7	0.03	20	10
Myrica pennsylvanica	0.7	0.0	10	0
Smilax glauca	0.4	0.1	60	20
Quercus stellata	0.4	1	10	30
Sassafras albidum	0.06	0.5	10	50
Vaccinium angustifolium	0.05	0.0	10	0
Myrica peregrina	0.03	0.2	10	10
Quercus velutina	0.0	2.5	0	90
Pieris mariana	0.0	0.8	0	20
Quercus montana	0.0	0.2	0	20
Chimaphila maculata	0.0	0.03	0	10
Kalmia angustifolia	0.0	0.4	0	10

TABLE III. *Summary of total values in the two stands with the differences calculated. Cover and open space values are from transect data; basal area and tree density values are from quadrat data.*

Value		Pine stand	Oak stand	Difference
Total tree cover	cm	42,595	103,880	61,285
	%	43	104*	61
Total open space in the tree canopy	cm	57,935	15,780	42,155
	%	58	16	42
Total basal area in sq ft per 2,500 sq m		37.2	41.5	4.3
Total tree density per 2,500 sq m		128	234	106
Per cent average light penetration at 2 m		68	29	39
Total shrubby cover	cm	18,687	16,075	2,612
	%	93	80	13
Total open space in the shrub layer	cm	5,920	6,735	815
	%	30	34	4

* Per cent higher than 100 reflects overlapping of the crowns of trees.

average around two meters in height. Of these species, *Q. ilicifolia* is the most important, contributing 20 per cent of the total shrubby cover and occurring on 80 per cent of the transects.

The continuity of the shrub layer can be determined from the data on total shrubby cover and open space in table III. The total shrubby cover is 93 per cent with 30 per cent open space in the 200 meters of transects. Thus 23 per cent of the shrub cover is due to overlap of shrub canopies. The average length of the open spaces is under 50 centimeters.

An herbaceous layer is virtually nonexistent in this community. Observations at several other times during the growing season indicate that herbaceous species are rare. Of those that were found, the following are the more important: *Carex pennsylvanica, Melampyrum lineare, Andropogon scoparius, Pteris aquilina, Panicum addisonii, Helianthemum canadense, Gnaphalium polycephalum* and *Polygonella articulata.*

A high cover of lichens and mosses is present on the surface where the mor humus layer is thin or absent. Although lichens and mosses were not studied quantitatively it was obvious that the lichens were of greater importance. Neither of these populations was studied.

The oak stand.—The oak stand is a rather homogeneous community of oaks with a small amount of pine (fig. 3). The almost continuous shrub layer is composed primarily of ericaceous species with a small amount of cover contributed by the reproduction of the oaks. The scrub oaks are not abundant in this stand.

a. The tree layer. Chestunt oak, *Quercus montana,* and black oak, *Q. velutina,* are the dominant members of the tree canopy, contributing 42 per cent and 38 per cent of the total tree cover, respectively. As can be seen from the quadrat

FIG. 3. Photograph taken in the oak stand, winter aspect.

TABLE IV. *A comparison of data for the tree layer on frequency, density (numerical abundance), basal area, and cover as obtained by the quadrat (Q) and the transect method (T). Column labeled DIF shows how much greater or less T is than Q. Total area of quadrat sample = 2,500 square meters in each stand; total linear distance in transect sample = 1,000 meters in each stand*

Species	Per cent frequency			Per cent of total density and numerical abundance			Per cent of total basal area			Per cent basal area, Q, vs. per cent cover, T		
	Q	T	DIF	Q	T	DIF	Q	T	DIF	Q	T	DIF
Pine stand												
Pinus rigida	100	92	− 8	76	76	0	82	73	− 9	82	70	−12
Pinus echinata	20	7	−13	5	4	− 1	6	6	0	6	7	+ 1
Quercus stellata	20	10	−10	8	4	− 4	5	2	− 3	5	4	− 1
Quercus marilandica	32	10	−22	8	3	− 5	0.2	0.2	0	0.2	2	+ 1.8
Quercus velutina	8	26	+18	2	10	+ 8	6	17	+11	6	14	+ 8
Sassafras albidum	4	2	− 2	1	1	0	0.1	0.3	+ 0.2	0.2	1	+ 0.8
Quercus alba	0	2	+ 2	0.0	0.6	+ 0.6	0.0	2	+ 2	0.0	2	+ 2
Oak stand												
Quercus montana	100	94	− 6	51	44	− 7	41	31	−10	41	42	+ 1
Quercus velutina	76	94	+18	23	35	+12	34	42	+ 8	34	38	+ 4
Pinus rigida	84	72	−12	22	16	− 6	24	23	− 1	24	16	− 8
Quercus stellata	12	18	+ 6	3	3	0	0.8	0.3	− 0.5	0.8	1	+ 0.2
Quercus marilandica	8	0	− 8	1	0.0	− 1	0.2	0.0	− 0.2	0.2	0.0	− 0.2
Sassafras albidum	4	0	− 4	0.4	0.0	− 0.4	0.01	0.0	− 0.01	0.01	0.0	− 0.01
Quercus alba	0	2	+ 2	0.0	0.3	+ 0.3	0.0	0.3	+ 0.3	0.0	0.2	+ 0.2
Pinus echinata	0	10	+10	0.0	1	+ 1	0.0	3	+ 3	0.0	2	+ 2

data in table IV, *Q. montana* forms 51 per cent of the total tree density, 41 per cent of the total basal area, and has a frequency of 100 per cent. *Q. velutina* forms 23 per cent of the total density, 34 per cent of the total basal area, and has a frequency of 76 per cent. *Pinus rigida* is obviously of secondary importance, but still contributes 16 per cent of the total tree cover, 24 per cent of the total basal area, and 22 per cent of the total tree density. It has a frequency of 84 per cent. *Quercus stellata* and *Q. marilandica,* the smaller oaks, are relatively unimportant in the community. There is a small number of individuals of *Sassafras albidum, Quercus alba,* and *Pinus echinata* in the community but they contribute little to the tree canopy.

The community presents a nearly continuous canopy (table III). The total tree cover is 104 per cent (20 per cent overlap of canopies) with 16 per cent of open space in the 1,000 meters of transects. The openings in the tree canopy averaged less than 2 meters in length and were well distributed along the 1,000 meters sampled.

b. *The shrub and herb layers.* In this community, the shrubby layer is of rather uniform height, slightly over a meter, and quite homogeneous. The ericaceous shrubs contribute almost 90 per cent of the total shrub cover (table II). Of these, *Gaylussacia baccata, G. frondosa,* and *Vaccinium vacillans* are the most important. These species contribute 39 per cent, 28 per cent, and 21 per cent of the total shrub cover, respectively.

All other species are relatively unimportant, none forming 3 per cent or more of the cover. *Gaultheria procumbens* is the most important with 2 per cent. This species occurs in scattered patches under the taller shrubs. The only other shrubs forming more than 1 per cent of the cover are *Quercus prinoides* (2 per cent) and *Q. ilicifolia* (1 per cent). Arborescent reproduction is included in the shrub layer, and that of the two oaks, *Quercus velutina* and *Q. montana,* contributes slightly more cover than do the scrub oaks.

The continuity of the shrub layer can be seen from the data in table III on total cover and open space. The total

shrubby cover is 80 per cent, and the open spaces amount to 34 per cent of the 200 meters sampled. The average length of the gaps in the shrub layer is over 100 centimeters.

Herbaceous species are rare and widely scattered. Of those observed, not necessarily at the time of sampling, the following are the most abundant: *Andropogon scoparius, Panicum addisonii, Pteris aquilina, Tephrosia virginiana, Carex pennsylvanica, Cypripedium acaule, Panicum virgatum, Baptisia tinctoria,* and *Stipa avenacea.*

A rather heavy cover of mosses and lichens is found in the few places where the mor humus is thin or absent. In this community, in contrast to the pine stand, the mosses are the more important. Neither population was studied.

Relation between tree and shrub layers.—An effort was made to study the relationship between the tree canopy and the shrub layer by attempting to correlate the open spaces in the tree canopy with the cover of the various species of shrubs. Since the shrub transects were situated directly under the first 20-meter segment of each of the ten 100-meter tree transects, the tree canopy and shrub cover could be investigated in relation to each other. Although the number of such related transects is too small for definite conclusions, it was felt that the results of the study were worthy of inclusion.

In the pine stand, on the basis of the data shown in figure 4, there is a general decrease in total shrubby cover as the open space in the tree canopy increases. However, in the oak stand (fig. 4), the trend is reversed; as the open space in the tree canopy increases, the total shrubby cover increases. The two curves not only differ in direction of slope, but differ in shape also.

The total cover for three species of shrubs was plotted against open space in the tree canopy for the oak stand. The curve for *Gaylussacia baccata,* which contributes most to the shrub cover, approximates the general shape of the curve for total shrubby cover in the oak stand, showing a decrease in total cover as open space in the tree canopy decreases. The curve for *Gaylussacia frondosa,* on the other hand, shows a decrease in total cover for this species as the open space in the tree canopy increases. *Vaccinium vacillans* shows no similarly well-defined distribution in the community.

No well-defined curves could be shown for any of the three dominant shrubby species in the pine stand. However, when total cover of *Gaultheria procumbens* is plotted against total open space in the tree canopy, total open space in the taller shrub canopy, and the sum of these two, well defined curves are evident, indicating a marked decrease in cover for this species with increased open space of both layers.

Age of the trees of the two communities.—On the basis of ring counts of increment borings in the two stands, the pine stand was found to be somewhat younger than the oak stand. Twenty-one oaks and four pines were sampled in the oak stand. These oaks ranged in size from 2.8 inches dbh to 17.4 inches dbh. The oaks in the community appear to fall into three age classes. The two younger groups are obviously of sprout origin. The trees in the youngest group average about 3.5 inches in diameter and about 30 years in age. The oldest individuals had 33 rings, indicating the approximate date of the last fire. The second group consists of trees about 6–8 inches in diameter with about 63 annual rings. It is possible that they represent growth following an earlier fire. The dominant oaks in the community are trees up to 17 inches in diameter. All have over 100 rings with a maximum of 129. Only the larger pines in the oak stand were sampled. They averaged over 100 years in age with a maximum ring count of 110 rings.

In the pine stand twenty-three individuals were bored. Of these, five were oaks, only the larger being chosen. The average diameter of these was around

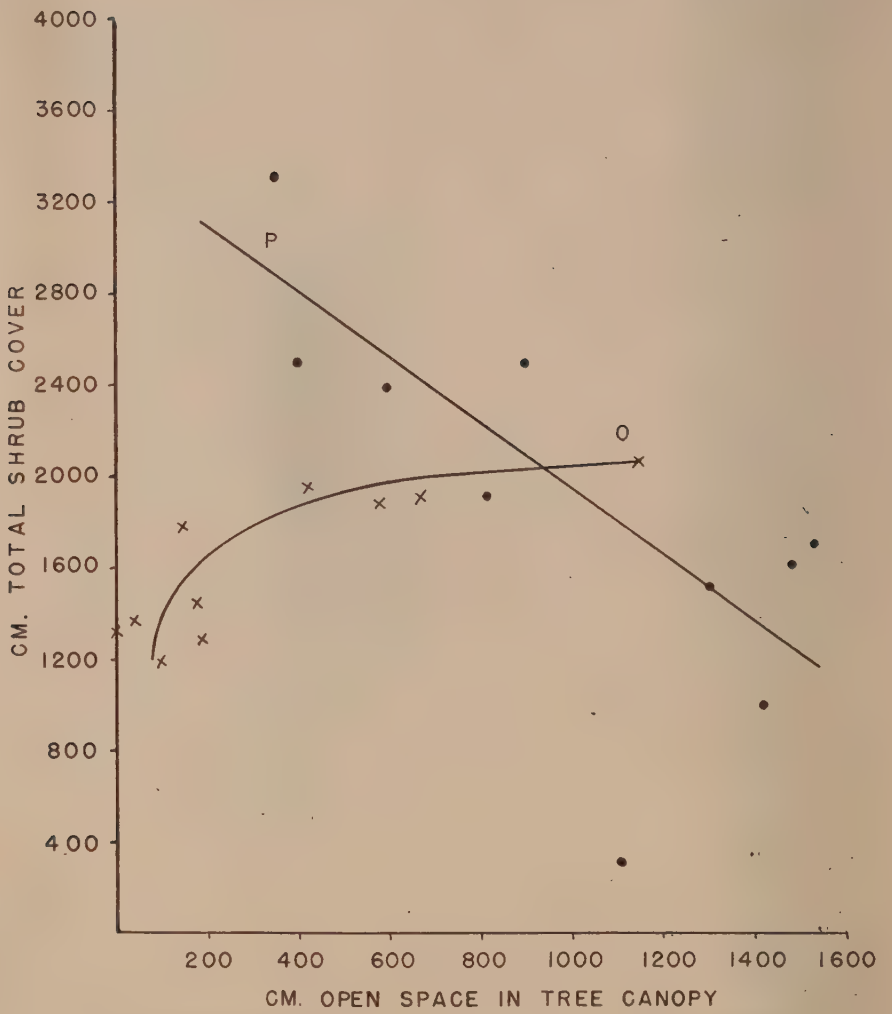

FIG. 4. Curves showing relationship of total shrub cover to open space in tree canopy. Curve P is for the pine stand, curve O is for the oak stand.

13.5 inches. The average number of rings was about 85 with a maximum of 92. The larger-sized pines, those over 10 inches dbh, averaged 64 rings. All the trees of *Pinus echinata* had between 70 and 75 rings. On the other hand, *Pinus rigida* showed an average of 56 rings but had a range from 45 to 77. The trees in the smaller-sized classes ranged in diameter from 3.4 to 8.5 inches, and varied from 16 to 66 rings. Only one tree showed more than 47 rings.

Comparison of the two methods of sampling

In comparing the data obtained by the transect method with those obtained by the quadrat method it should be emphasized that the number of individuals sampled by the two methods is not the same. The number of individuals counted in the quadrat method includes only those trees which were rooted in the quadrats. In the transect method, all individuals which

contributed cover to the transect were counted. The quadrat sample in the pine stand contained only 81 per cent of the number of individuals included in the transect sample. In the oak stand the quadrat sample contained only 65 per cent.

Frequency.—By noting the per cent of the ten 100 meter transects and the per cent of the twenty-five quadrats on which a species occurred, frequency data were obtained for the two methods. As Gleason ('29) has pointed out, frequency values are dependent upon quadrat size. Just how comparable the transects and the quadrats are as sampling units is not known. If the number of individuals sampled is the only criterion, then the transect method sampled a larger segment of the population. In comparing the frequencies in table IV, it can be seen that the frequency values obtained by the transect method are somewhat higher for *Quercus velutina* in the pine stand and *Q. velutina* and *Q. stellata* in the oak stand. As would be expected the tree species with the larger-crowned individuals show the larger increase in per cent frequency with the transect method.

Density.—In the quadrat method of sampling, density is the number of individuals per unit area. To get comparable figures on the relative numerical abundance of the species from the transect method, all individuals contributing cover were counted (Bauer '43). In order to compare the two methods, the numerical abundance, "density," of each species is given as the per cent of the total for all species. From the data in table IV, it is at once obvious that *Quercus velutina* which has the largest crown area gains the most in per cent of the total "density" when the transect method is used. In the pine stand, *Quercus stellata* and *Q. marilandica* show the greatest loss in per cent of total "density" while in the oak stand, *Quercus montana* and *Pinus rigida* show the greatest loss. ("Loss" and "gain" are used here in comparing the transect against the quadrat data. Inspection of table IV will clarify this usage.)

Basal area.—Determination was made of the diameter at breast height of all individuals contributing cover on the transect line as well as of all individuals whose stems arose in the quadrats. From these measurements basal area was obtained from tables. The values for each species are expressed as per cent of the total computed basal area for all species in each stand. A comparison of the data obtained on the quadrats with that from the transects can be seen in table IV. In terms of per cent of total basal area of all species in the pine stand, *Pinus rigida* shows the greatest loss while *Quercus velutina* shows the greatest gain when the transect method was used. However, in terms of the individual species, *Quercus stellata* shows fifty-seven per cent less basal area by the transect method. In the oak stand, the greatest loss is shown by *Quercus montana* and *Pinus rigida* and the greatest gain by *Quercus velutina.* Based on the individual species *Quercus stellata* again shows the greatest loss.

Basal area vs. cover.—In most studies of the tree layer, basal area is used as the method of indicating dominance among the tree species. In comparing basal area computed from the quadrat data with cover obtained from the transect data there is a noticeable shift in values (table IV). In the pine stand, *Pinus rigida* has a much lower per cent of total cover than it has of total basal area. *Quercus velutina,* a tree with a large spreading crown, shows the opposite trend. In the oak stand, *Pinus rigida* and *Quercus velutina* show the same cover-basal area trends as in the pine stand. *Quercus montana* has a higher per cent of cover than of basal area.

The differences represented in the last column of table IV represent the differences in relative dominance that result when per cent basal area obtained from twenty-five 10×10-meter quadrats is used for the criterion as opposed to that

based on the results of per cent cover on ten 100-meter transects.

Light

The results of the light study in the two stands indicate that the canopy in the pine stand permits the passage of considerably more light than the canopy in the oak stand. The average light reaching the 2 meter level in the pine stand is 68 per cent of full sunlight whereas in the oak stand it is only 29 per cent.

The distribution of light in the two communities can be seen in figure 5. In the pine stand 14 per cent of the readings are under 10 per cent of full sunlight, with 8 per cent showing less than 6 per cent of full sunlight. Over 50 per cent of the readings are 50 per cent or more of full sunlight and 41 per cent show 80 per cent or more of full sunlight.

In the oak stand, 50 per cent of the readings indicate less than 10 per cent light penetration with 37 per cent showing less than 6 per cent penetration. Twenty-two per cent of the readings show over 50 per cent penetration and 20 per cent were 80 per cent or more of full sunlight.

Soils

Both of the communities studied occur on light sandy soils exhibiting podzol profiles. The soil in the oak stand has been mapped as Sassafras sand, whereas the pine stand occurs near a transition area

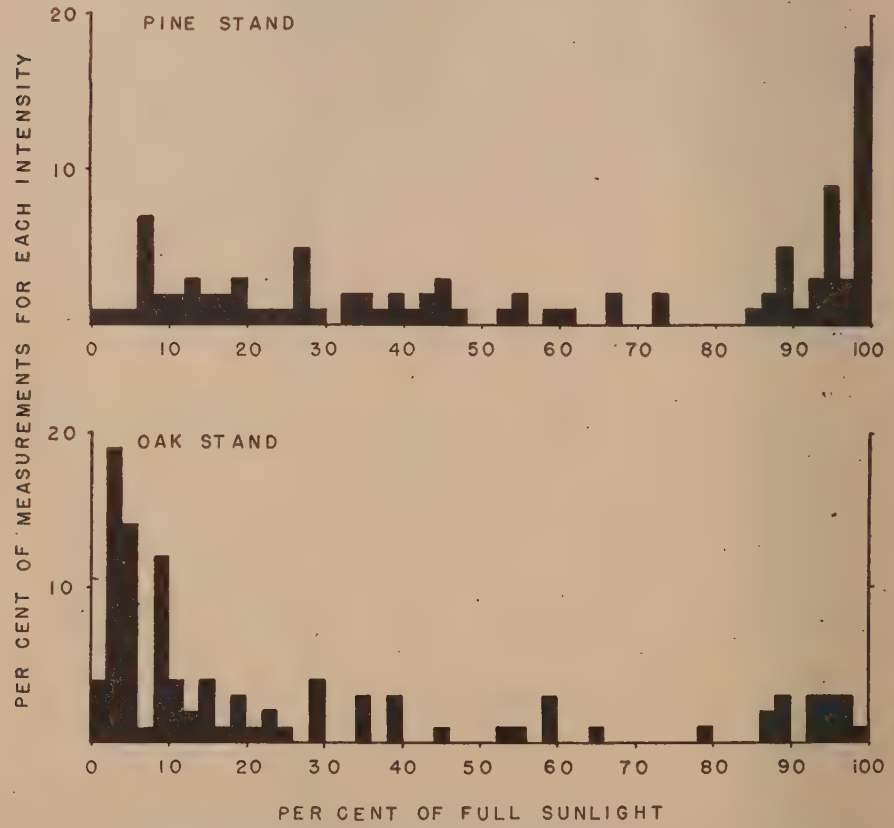

FIG. 5. Graphic presentation of the distribution of the light intensity at the two meter level in the two stands.

between Sassafras sand and Lakewood sand (Lee '23). The profile characteristics and the soil texture differ somewhat between the two areas. The markedly bleached part of the A horizon, composed of gray sand, is but 8 centimeters deep in the oak stand, whereas it is about 40 centimeters deep in the pine stand. The soil in the oak stand contains more of the finer fractions than that of the pine stand. Mechanical analyses were made of the A1 and the B2 horizons. They indicate the A horizon of the pine stand to be 97.0 per cent sand, 1.5 per cent silt, and 1.5 per cent clay, while the A horizon in the oak stand is 92.7 per cent sand, 5.7 per cent silt, and 1.6 per cent clay. The B horizon in the two stands is an orange to orange-brown sand containing appreciably more silt and clay. The mechanical analyses of the lower part of the B horizons indicate 95.3 per cent sand, 1.1 per cent silt, and 3.6 per cent clay for the pine stand, while in the oak stand the values for this horizon were 88.0 per cent sand, 5.3 per cent silt, and 6.7 per cent clay. This heavier part of the B horizon is 22 centimeters thick and begins at a depth of 23 centimeters in the oak stand and in the pine stand it is 20 centimeters in thickness and starts at a depth of 50 centimeters.

Discussion

Vegetation

The exact nature of the climax vegetation of the pine barrens has been subject of considerable debate. Pinchot ('99: 109) describes an old growth forest of this area as being a heavy growth of pines 150–200 years old and 15 to 20 inches in diameter, with occasional trees as large as 24 or even 30 inches. However, his data disclose a heavy growth of young oaks and an occasional hickory. In fact, *Quercus alba, Q. velutina,* and *Q. montana* make up 70 per cent of the total tree density on the one acre studied by Pinchot. He termed this stand an original forest, but at the present time, the local foresters consider that it was merely old second growth. Stone ('11: 69), in pondering the problem of the natural vegetation, states that "There are woods of rather tall pine with practically no oaks of any size, but with an undergrowth of scrub oaks and huckleberries. Then there is a more open growth [referring to relative freedom from heavy undergrowth] in which oaks and pines mingle in about equal proportion and in which the oaks, mainly *Quercus marilandica,* reach a fair height. Other sections are covered with a dense growth of oaks including *Q. prinus* [montana], *Q. alba, Q. marilandica, Q. ilicifolia,* and *Q. velutina.* It seems to me that the first two types are the natural or primitive ones while the solid oak growth covers recent clearings. The pines spring up again in such tracts and reassert themselves unless fire or continuous clearing have exterminated them." Taylor ('12) seems to believe that the pine forests of the region have been the natural upland vegetation since upper Miocene times. Harshberger ('16: 49) states, concerning succession in the pine barrens, "When a pine forest is destroyed by fire, or the trees removed in lumbering operations, it may be succeeded by a scrub-oak thicket. This in turn is replaced by a coppice of taller trees which, when admixed with pitch-pines, can be designated the Mixed Pine-Oak Formation. The pines may ultimately suppress the oaks, and the vegetation returns to the original pine forest in which the series is bound sooner or later to culminate."

More recent investigations, conducted for the most part by foresters, do not support the idea of a pine climax. Little and Moore ('49) state that ". . . the successional trend is toward a hardwood forest. In the absence of cutting and fire, the pines would apparently form an exceedingly small part of subsequent stands if they occurred at all." These authors cite the work of Stevens ('40) as the best available evidence of the climax forest of the region. On the basis of Stevens' work, they state that these forests ". . . may be composed

largely of black, white, scarlet, and chestnut oaks (*Quercus velutina, Q. alba, Q. coccinea, Q. montana*), although other hardwoods, particularly hickory (*Carya*) and red maple (*Acer rubrum*), may be minor components."

The earliest written descriptions of the upland vegetation of the region report a predominance of pine forest and smaller amounts of pine-oak forest as indicated by Moore ('39). Moore ('39) and Little ('46) both state that the only logical explanation for the predominance of pine in the original forests of the region is the frequent occurrence of light fires, presumably Indian in origin. This theory can neither be proven nor disproven but as Carter ('50) has said, the magnitude of early man's influence upon his environment is little appreciated. All fossil evidence of man in North America is associated with evidence of fire. There is no reason to believe that early man had any better aesthetic appreciation of the effect of fire on native vegetation than does modern man. In fact, there appears to be evidence that the American Indian actually used fire to facilitate hunting.

Potzger ('45) constructed pollen profiles of several bogs in and around the pine barrens of New Jersey. The results of his study seem to indicate that pine has been a major component in the vegetation of the region as far back as the pollen record goes. In the seven profiles located in the pine barrens proper, *Pinus* accounted for an average of 40 per cent of the tree pollen counted. *Quercus, Betula,* and *Castanea* are the three next most important genera represented in the profiles. These three account for about 45 per cent of the pollen, with *Quercus* constituting over half of this. It must be remembered in this connection that pine is over-represented in pollen spectra and oak under-represented (Cain '44). The age of these peat deposits is still unknown although it may be possible to date them by radioactive determination. However, it may be assumed that some of the records date back at least beyond the influence of white man, and may even represent forests of Wisconsin time, as Potzger believes. Deevey ('49) has published a word of warning in the interpretation of these profiles emphasizing that further work is necessary before they can be accepted at face value. The composition of the pollen profiles seems to substantiate the early accounts which describe the upland areas as being occupied by a mixture of oak and pine.

It is not possible to determine the species of *Quercus* which are represented in the profiles. Therefore, it is possible that an understory of scrub oak under pine could account for the high oak composition. However, since 6 per cent of the pollen is *Castanea,* and since this species requires a similar environment, it is probable that the larger oaks, *Quercus velutina, Q. alba, Q. montana,* and *Q. coccinea,* contributed some of the *Quercus* pollen.

When the work of these various investigators is fitted together, the following picture emerges. Pine has been a very important constituent of the forests of this region for a considerable length of time. Recent ecological study (Stevens '40) indicates that the oak-pine community is climax on these sandy Coastal Plain soils. Moore, Little and Allen, as previously cited, feel that the present and past existence of forests of high pine composition are due to fire relations. These authors feel that Indian hunting methods resulted in frequent light burnings.

From the work of these investigators, it will be assumed that the climax vegetation on these light soils is a mixed hardwood forest. However, the present authors agree with Stevens that scattered pines could be present in the climax in a status similar to that of *Pinus strobus* in the climax northeastern deciduous forests (Lutz and McComb '35). The differences in vegetation structure of the two communities can be studied from this standpoint.

The two stands occupy well drained, upland sites. The soil in both areas is sand, containing a minimum of 88 per

cent sand. Although the oak stand contains somewhat more silt and clay, it does not seem probable that the difference is of great enough magnitude to markedly influence the composition of the two communities. It seems reasonable to assume that the frequency and magnitude of past disturbances far outweigh the influence of differences in soil in the two communities.

It was not possible to obtain direct fire and cutting history much beyond thirty years ago. According to Mr. J. P. Allen, Supervisor of the Lebanon State Forest, neither of these areas has suffered from fire damage since his coming to the forest in 1929. He indicated, however, that eight to ten years prior to that time, a very light fire burned through the oak stand. The increment borings indicate that one group of oaks of sprout origin has about 33 annual rings, confirming Allen's statement. A second group with 63 rings suggests an earlier fire. Mr. Allen was unable to state how long ago the last fire occurred in the pine stand. However, there is indirect evidence in the vegetation. A pronounced age group of pines showing about 47 rings, as well as a fire scar on an oak, indicates that the last fire was in 1902.

Little states that pine-scrub oak communities occur on areas that have been burned more frequently than areas occupied by the oak-dominated forests. If severe fires occur frequently enough the species which do not produce seed until of large size are eliminated from the community except for occasional sprouts. *Quercus velutina, Q. alba, Q. montana,* and *Pinus echinata* are species of this nature. Those species which sprout vigorously and produce seed at an early age can persist in areas which are frequently burned. Most of the species in the pine stand are of this sort. Uneven-aged oak stands represent areas that have been burned periodically by fires of low enough intensity so that some of the individuals survive (Little '46).

The two communities studied correspond to a certain extent to the mixed oak type on the one hand and to a less extent to the pine-scrub oak type on the other hand. The pine stand has a few of the larger oaks whereas the oak stand is dominated by them. If the climax is a mixed hardwood forest, then the pine stand is much younger successionally than is the oak stand. The rare large individuals of *Quercus velutina* in the pine stand represent survivors of past fires and cuttings. They are at least ten years older than the largest pines. In the oak stand, the small sprout *Quercus montana* and *Q. velutina* together with small individuals of *Pinus rigida* (some of sprout and some of seedling origin) probably represent new growth following the light fires that have swept through the stand.

The increment borings indicate the dominant individuals in the pine stand to be over sixty years old. The absence of seedlings and saplings of *Quercus montana* and *Q. velutina* in the shrub layer suggests a considerable lag in the establishment of these species. In the oak stand, all the arborescent oaks were reproducing as were the pines. Pine reproduction in the seedling and sapling classes was not as abundant as that of the arborescent oaks. The present vigor of the young pine, however, gives no indication that it will not continue to be present in the oak stand. At least under present circumstances neither light conditions nor root competition is inhibiting pine reproduction.

There are fewer individuals of *Quercus marilandica* and *Q. stellata* in the oak stand than there are in the pine stand. Reproduction of these two species may be inferred from the data in table II on cover contributed to the shrub layer. *Quercus stellata* was not important in the seedling and sapling class in either stand. Slightly more cover was contributed by this species in the oak than in the pine stand. Reproduction of *Q. marilandica* was much heavier in the pine stand. It would seem that both of these species become less

important as the succession progresses. If one were to classify the arborescent oaks concerned in order of their mesophily, *Quercus marilandica* and *Q. stellata* would be the most xeric, *Q. coccinea* and *Q. velutina* would come next, then *Q. montana* and finally *Q. alba* as the most mesic.

The shrub layer in the oak stand differs from that of the pine stand primarily in the lower scrub oak cover (*Quercus ilicifolia* and *Q. prinoides*). Another difference, also, is the greater cover of *Gaylussacia frondosa* in the oak stand and of *Gaultheria procumbens* in the pine stand. These differences, together with the presence of small numbers of *Pieris mariana, Chimaphila maculata,* and *Kalmia angustifolia* in the oak stand, may indicate this community to be less far removed from climax.

The results obtained from comparing open space in the tree canopy with total shrub cover, though inconclusive, are interesting. The fact that these data indicate an inverse relationship in the oak stand and a direct relationship in the pine stand should be looked into further. It is to be expected that as a tree canopy becomes more closed, thus permitting less light to penetrate to the shrub layer, a point will be reached when the shrub layer will suffer from lack of sufficient light. On the basis of the data represented in figures 4 and 5, the tree canopy in the oak stand seems to have developed to the point where in some parts it prevents the full development of the shrub layer.

The inverse relationship of total shrub cover and open space shown in figure 4 for the pine stand may or may not have anything to do with light. The average light penetration in the pine stand was 68 per cent of full sunlight and 52 per cent of the measurements indicated 50 per cent or more of full sunlight. Only 14 per cent of the measurements showed less than 10 per cent of total sunlight (fig. 5). The area in which the shade of the tree canopy might become limiting to the shrub layer is small indeed. The distribution of the shrubs may in part be a result of past fire damage to the mor humus layer. Areas in which the mineral soil has been exposed may not be as congenial for the establishment of ericaceous shrubs. Since the humus layer is restored more rapidly under the trees due to leaf litter accumulation, it may be that these shrubs show a tendency to become reestablished sooner where the tree canopy is more continuous. In the very sandy soils characteristic of the region, shade from the tree canopy may also have a beneficial effect in the water relations of the upper layers of the soil. However, further study is necessary to determine the validity of this inverse relationship.

Comparison of the two methods of determining dominance

Many previous investigators have stressed the importance of cover as a criterion for expressing dominance among species (Clements '05, Rommell '30, Braun-Blanquet '32, Bauer '36 and '43, and Penfound '45 among others). In the study of herbaceous and shrubby vegetation, cover has been widely used, but in arborescent communities, foresters commonly use volume of standing timber while most ecologists use basal area to express dominance. However basal area is not considered as valuable a criterion as cover. A given basal area per unit area may represent a closed canopy formed by a dense growth of young individuals or a much more open stand of older and larger trunks. Basal area, though it may be valuable in determining dominance, is not always the best measure of the influence of the tree layer upon the species existing below.

Penfound ('45) studied the relationship of the trunk diameter to crown diameter. He states that in three forest types in the New Orleans area the dbh of the trees averaged 6.5 per cent of the crown diameter with a range of from 3 to 9 per cent. Just how reliable this ratio would be for other parts of the country is not known, but there are certainly many columnar

species and many broad crowned species that would extend the range of this ratio somewhat further. How this ratio may vary between individuals of the same species but of different ages is also an important factor.

The use of cover in studying arborescent communities has not received a great deal of attention in ecological studies. Cain ('36) has used cover in describing a forest on Long Island. He obtained tree cover by ocular estimate and expressed it in terms of cover classes. The difficulty of measuring cover in such communities has, no doubt, been the greatest handicap. Anyone who has attempted to estimate the per cent of cover on a 10 × 10-meter quadrat of the various species in a layered tree canopy is well aware of the difficulty involved in obtaining reliable data. For this reason, the transect method as used by Bauer ('36 and '43) in California chaparral was adapted for use in the present study.

In the present study, the results obtained by the transect method essentially as outlined by Bauer are compared with frequency, density, and basal area data obtained by the quadrat method. It was anticipated that the two methods would produce different pictures of the communities. As can be seen in table IV, the magnitude of these differences is great enough to be of importance. When dominance among the species is based upon cover instead of basal area, the broad crowned species gain considerably over those with more columnar crowns (see *Quercus velutina* in the last column of table IV). It seems logical that species with broad crowns exert an influence over a greater area, and therefore should be given greater weight in community dominance than narrow crown species. For species with more intermediate crowns relative dominance remains the same regardless of whether basal area or cover is used.

Bauer ('43), after studying aggregations of cards, suggested that the transect method can be utilized to obtain data on both frequency and numerical abundance as well as on cover. When he compared the results of the transect data with those obtained on the same card aggregations by the quadrat method, his data indicated good agreement between the two methods. In the present study, however, a comparison of the two methods shows that the species with large crowns gain considerably in both frequency and per cent of total "density" when the transect method was used. This indicates that the larger-crowned species are favored by the transect method.

Penfound ('45), also studying aggregations of cards, states concerning quadrat sampling ". . . it became evident that the determination of frequency and density could not be based on the fractional parts of cards falling within the squares. When this was done, we sampled a given card in as many as four contiguous quadrats. From these data we obtained considerably higher frequencies and densities than might be expected from the actual number of cards on the table. Therefore, all determinations on frequency and density were made on the basis of the central circles of the cards (trunks) only." The present authors agree with Penfound that presence in a quadrat must be based upon trunks rather than crowns. This is true whether quadrats are contiguous or not. Large-crowned species reach over the quadrat boundary while small-crowned species rooted the same distance or less away are not represented. Thus, frequency and density data based upon fractional parts of crowns will favor large-crowned species. Canfield ('41) indicates that this disproportionate representation was recognized by Klapp in 1934.

In community analyses of forest vegetation, the occurrence of an individual in a quadrat for obtaining frequency and density data is usually limited to those individuals rooted in the quadrats. Bauer's frequency and numerical abundance ("density") data were calculated from the occurrence of crowns and fractional parts of crowns in the quadrats.

This difference in concept of the occurrence of an individual in a quadrat is the cause of the discrepancy between Bauer's work and that of the present authors. Though Bauer's results indicate good agreement between the two methods, it should be pointed out that this agreement arises from an altered concept of occurrence in a quadrat. Thus frequency and density data obtained by the transect method are not equivalent to those obtained by the quadrat method commonly used in forest studies.

Ashby ('48) states that "Among miscellaneous contributions to the technique of statistical ecology may be mentioned the work of Bauer who reached, with the aid of 1000 coloured discs, the not unexpected conclusion that transects can be used instead of quadrats for sampling communities; . . ." This would leave one to assume that Ashby fails to appreciate the differences in results obtained by Bauer's transect method as opposed to the quadrat method.

Dr. W. E. Gordon, of the Nashville School of Social Work, in conversation with the senior author, has suggested that the square of the linear measurements should be used as a basis for indicating cover. This is based on the fact that cover is in reality the area of the projected crown, and area would be more nearly proportional to the square of the linear measurements. In order to test the influence of this relationship all linear measurements for the tree layer in each community were squared prior to calculating per cent cover. These values were compared with those given in table IV. Thus it was possible to ascertain the order of magnitude of the difference in per cent cover as indicated by the two methods. It was found that the larger-crowned species gained in per cent cover while the smaller-crowned species lost. In the oak stand, the greatest increase in per cent cover was shown by *Quercus velutina* which demonstrated a gain of 6 per cent. The greatest decrease was shown by *Pinus rigida* which demonstrated a loss of 5 per cent. The same tendency was shown by these species in the pine stand.

Since per cent cover is more proportional to the squared values than to the linear measurements, it would be advisable in the interests of greater accuracy to square the measurements. However, in the two communities studied the greatest difference is of a small order of magnitude. It may be questionable whether the greater degree of accuracy is worth the labor. In other communities the differences may be of such order of magnitude as to leave no question.

In attempting to evaluate these two methods, the following points may be made:

1. The quadrat method using 10×10 meter-quadrats has been widely used in sampling the tree layer. Reliable frequency, density and basal area data may be obtained quickly by this method.

2. Determination of cover for arborescent species is difficult and inaccurate when the quadrat method is used.

3. The transect method using the cover sight permits the easy determination of cover in arborescent communities.

4. The transect method permits the easy determination of open space in the tree canopy for use in studying light and tree-shrub-herb relationships.

5. Data on frequency, numerical abundance, and basal area that are obtained by the transect method are weighted in favor of the large-crowned species.

6. The transect method is considered to yield more valuable data than the quadrat method. Thirty-six man hours were required on the twenty 100-meter transects that intercepted 512 trees; eighteen man hours were required on the fifty 10×10-meter quadrats containing 362 trees. However, the transect method permitted measurement of tree cover, and open space in the tree canopy. It yielded somewhat less adequate figures on frequency, numerical abundance and basal area. The quadrat method yielded only frequency, density, and basal area data.

Although basal area is the most valuable of these three, it fails to indicate the degree of shading as effected by crown spread nor does it indicate much of anything about the open spaces between crowns in the canopy. Cover does show these. In view of the greater value of cover data in community analysis (Penfound '45), and the added value of being able to determine accurately open space in the canopy, the transect method appears to be superior.

Summary

1. The structure of the vegetation of two upland forest communities occurring near the center of the Pine Region of New Jersey is compared. Frequency, density, basal area and cover data are presented.

2. The two communities occur in the same general area and on similar soil types. The major causal factor in determining the difference in community composition seems to be age as influenced by fire history.

3. The younger community is composed primarily of *Pinus rigida* and *P. echinata* with smaller amounts of *Quercus velutina, Q. stellata* and *Q. marilandica.* The understory is a mixture of ericaceous shrubs and scrub oaks.

4. The older community is composed primarily of *Quercus montana* and *Q. velutina* with smaller amounts of *Pinus rigida, Quercus stellata* and *Q. marilandica.* The understory is composed primarily of ericaceous shrubs.

5. The two communities seem to represent two stages in the succession toward the climax vegetation of the light Coastal Plain soils of the region. Their present status is probably a result of differential disturbance due to fire.

6. The quadrat method was used to obtain frequency, density and basal area for the species of the arborescent layer. The transect method was used to obtain cover, open space, basal area, frequency, and numerical abundance for the species of the tree layer and cover and open space for the species of the shrub layer.

7. A cover sight is described which permits accurate measurement of cover and open space in the tree canopy.

8. Dominance among the species in the tree layers, as indicated by per cent of total cover and per cent of total basal area, is compared. The use of cover instead of basal area, for expressing dominance, favors the large crowned species. This tendency is accentuated when linear measurements are squared.

9. Frequency, density and basal area obtained by both methods are compared. The transect method results in a greater per cent of all three values for the species having large crowns.

10. Relationships between open space in the tree layer and shrubby cover are implied, but the data on these relationships are inconclusive.

11. In view of the greater value of cover as compared with frequency, density, and basal area in expressing community structure and in view of the possibility of accurate measurement of open space for use in studying tree-shrub-herb relationships the transect method shows promise.

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BIRD POPULATIONS OF THE HIGHLANDS (NORTH CAROLINA) PLATEAU IN RELATION TO PLANT SUCCESSION AND AVIAN INVASION[1]

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Birds, during the breeding season at least, are proving to be favorable subjects for the study of population dynamics in nature. Their conspicuousness and territorial behavior aid population measurements and make birds especially promising material for the study of competition, habitat selection, niche relations, and the relation of population density to plant succession, distributional changes, and to speciation. The study of wild bird populations in North America in recent years has been influenced by two important trends: (1) the development of the spot-mapping technic (see summary by Williams, '47), and (2) the increasing emphasis on population measurements of definitely delimited areas which are ecologically uniform or represent single, rather than mixed, communities. The annual "Breeding Bird Census" sponsored by Audubon Magazine, and subsequently Audubon Field Notes, for the past 12 years has particularly accelerated the latter trend. Although population estimates made with comparable technic are now available for a variety of communities in many biotic regions of North America, many gaps, both regional and ecological, must be filled before the student of populations can profitably analyze the results for elucidation of the basic problems mentioned above. Population measurements of major communities of the southeastern United States are especially needed, since few censuses from this region have been published. During the 12-year period previously mentioned, censuses from only 13 community areas have been published for the entire southeastern region (10 states): several states in other regions have contributed this number in a single year.

As part of a regional program of research on the comparative vertebrate ecology of mountains, piedmont, and coastal plain of southeastern United States, the objectives of the present study were threefold: (1) to determine bird population density of important communities of a high altitude region representative of the southern end of the Appalachians; (2) to relate bird populations to plant succession; and (3) to compare these data with those from other regions. An added incentive for this study arose from our desire to see if the density of population, or "population pressure," had any bearing on, or was correlated with, the recent rather spectacular invasion of several species from the mountains to piedmont (Odum and Burleigh, '46; Odum, '48).

THE HIGHLANDS PLATEAU

The Highlands Plateau is a high-altitude region with an elevation averaging approximately 4,000 ft. located on the main Blue Ridge of the Appalachian Mountains where North Carolina joins Georgia and South Carolina. The Blue Ridge extends into Georgia as a rugged ridge with a number of peaks between 4,000 and 5,000 ft., but there are no extensive, relatively flat areas at high elevations south of the Highlands Plateau, which thus occupies a strategic position near the end of the mountain salient which "funnels northern species into the heart of the southland," as it were. For this reason and because of the facilities offered by the Highlands Biological Lab-

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FIG. 1. Vegetative zonation on the Highlands Plateau. The lower dark belt is a mature hemlock-northern hardwood stand while the upper lighter colored area is an oak-chestnut forest growing on the drier slopes and summits.

oratory, the Highlands region was selected as a suitable region for the study of bird populations under mountain conditions.

The general plant ecology of the region is well illustrated by figure 1. There is no spruce zone at Highlands such as is present further north on the Blue Ridge or on the Great Smoky Mountains. The peaks (several exceeding 5,000 ft., elevation) and steeper slopes are covered with a deciduous forest, largely oak-chestnut, which is the probable climatic climax. The communities containing plants and animals with northern affinities are found in ravines, moist areas along streams, and high, level parts of the plateau. Hemlock is the chief dominant of this second major climax, probably to be considered a post-climax (Oosting and Billings, '39). The reason for this seemingly reversed zonation, which, incidentally, is characteristic of the southern Appalachians south of the spruce range, is that the relatively great difference in moisture between peaks and ravines is more important as a limiting factor for plants and animals than is the relatively small difference in temperature. Thus, red-breasted nuthatches and brown creepers, so-called Canadian Zone species, are to be found breeding in the lower, dark (hemlock) belt in figure 1, while birds of more southern origin may be found in the deciduous growth above them (light colored in fig. 1). Biotic communities, then, on the Highlands Plateau may be conveniently arranged in two series: (1) communities leading to the climax of oak-chestnut, the oak-chestnut sere, and (2) communities leading to the climax of hemlock or hemlock-birch, the hemlock sere. The former is largely deciduous throughout its development. Early successional stages in the latter may be entirely deciduous, but conifers develop at least a two-thirds dominance in the later stages of succession. The plant ecology of the virgin hemlock forests of the region has been studied by Oosting and Billings ('39), the occur-

rence and distribution of summer birds by Stevenson ('41), and distribution of small mammals by Odum ('49).

Methods

Three areas representing early, intermediate, and late or climax stages of succession were selected for each of the two principal seres of the region, making a total of 6 areas on which breeding bird populations were measured. Each of the areas is shown in figures 2 to 7 and they are designated in the subsequent discussion as follows: In the mesic or hemlock sere, (1) mesic shrubland (2) intermediate hemlock-hardwood (3) climax virgin hemlock; in the oak-chestnut sere, (4) xeric shrubland (5) intermediate deciduous forest (6) climax oak-chestnut. All of the plots have roughly the same altitude, between 3,800 and 4,100 feet, so that altitude is not a factor in determining differences in populations. Each plot selected was mapped, and outline maps were mimeographed. The area of each plot in acres was determined from the completed map by the use of a planimeter. Bird populations were determined by the spot-mapping or territory-mapping technic as follows: Each plot was visited in rotation for 3–4 hours in the morning and birds seen and heard while slowly cruising the plot were recorded on a fresh copy of the base map. Afternoon visits were also made to check questionable records and look for nests. Each area was visited from 4 to 6 times with total of 16 to 30 hours of observation. Total populations were calculated from the number of occupied territories plotted on composite maps. Each plot was censused for two successive seasons, except the oak-chestnut climax, which was censused only in one season. In 1946, observations were made between June 12 and July 4 and in 1947 between May 31 and June 25.

The size of some of the plots, especially the early seral stages, was smaller than originally planned because I was unable to locate large areas of uniform composition of desired stage in succession. In heavily forested mountain regions the total amount of early seral vegetation may be quite large, but it consists of numerous small areas, such as roadsides, small abandoned fields, etc. Plots of shrubland or young forest 25 or 30 acres in extent and of uniform composition just did not exist in the high altitude region. Consequently, since the object was to determine the population of specific communities for comparative purposes, it seemed desirable to select uniform, even though small, areas rather than diverse, but larger ones. Stewart and Aldrich ('49) report that extensive census work done on the Patuxent Refuge has shown that results from small uniform areas are more reliable than from larger mixed ones. However, small quadrats admittedly introduce errors in estimating abundance of less common species or those with large territories. Likewise, total density calculations may be exaggerated. Specifically, to test these possibilities for the region being studied, a 10-acre plot was measured in the center of the completed census map of the 25-acre oak-chestnut plot ac-

Table I. *The relation of plot size to density calculations in an oak-chestnut forest*

	Pairs per 100 acres based on: A 25-acre sample	A 10-acre sample
Ovenbird*	38	45
Black-throated blue warbler	24	25
Blue-headed vireo	22	30
Red-eyed vireo	12	15
Veery	12	10
Chestnut-sided warbler	8	15
Wood thrush	8	0
Towhee	6	0
White-breasted nuthatch	4	10
Downy woodpecker	4	5
Hairy woodpecker	4	0
Bl. and white warbler	4	5
Hummingbird	4	5
Ruffed grouse	2	5
Tufted titmouse	2	0
Carolina chickadee	2	0
Wood pewee	2	0
Robin	2	5

Total species, large area—18; small area—12

Total density (pairs per 100 acres), large area, 160.

Total density (pairs per 100 acres), small area, 175.

* For scientific names see table III.

tually censused. Populations were then calculated in pairs per 100 acres for both 10- and 25-acre plots, the results being shown in table I. It will be seen that the density of the five most abundant species is approximately the same whether calculated from the large or small area. For the less common and larger species the small plot either gives too high a figure or fails to record them at all. The total density as determined from the 10-acre plot is roughly 10% greater than for the large area. In conclusion, it appears that small plots may be used to determine density of the most common species but are less reliable for the less common species. If results from small plots are to be compared with those from larger ones, density calculations based on small plots should be corrected. Accordingly, in the data presented in tables II and III a 10% reduction in the density calculation of each species has been made, where plots were 10 acres or less in size. Where a pair's territory was not wholly on the study area, the appropriate fraction was carefully estimated from field observation and calculated density figure in pairs per hundred acres rounded off to the nearest whole number as further precaution against distortion of figures based on different sized samples.

The Study Plots

1. *Mesic shrubland* (fig. 2).—Size 6.4 acres, located four miles east of Highlands on Route 64 opposite and with similar topographic location as the plot of virgin hemlock (No. 3). The small stream which flows through the virgin area continues through the shrubland. The vegetation consists of shrubs and small trees chiefly alders, willows, and brambles (*Rubus*) which form dense thickets interspersed with more open areas dominated by grasses and herbs. Huge stumps of hemlock and thickets of laurel (*Kalmia*) and *Rhododendron* remain from the original hemlock forest which occupied the area. The plot has never been cultivated, but has apparently been subjected to some grazing in the past.

Fig. 2. Mesic shrubland which has developed after the logging of the climax hemlock-hardwood forest. Virgin undisturbed forest may be seen in the background.

FIG. 3. Interior of the intermediate hemlock-hardwood forest. Note hemlock and birch trees and well developed shrub understory.

2. *Intermediate hemlock-hardwood forest* (fig. 3).—Size 15 acres, located around the Highlands Biological Laboratory building and Lake Ravenel. Some of the hemlocks in the western and eastern portions are very large and probably are a part of the original forest, but most of the area is covered with a second growth, dominant trees averaging 6–10 inches D.B.H. The deciduous elements, chiefly birch and maple, and the coniferous elements, hemlock and white pine, are approximately equal in dominance. The understory is well developed and varies from pure *Rhododendron* along small streams to witch hazel and *Azalea* in the drier portions. The clearings immediately around the Laboratory building and between the Laboratory and Museum Building are not included in the area censused since they obviously represent an entirely different community.

3. *Virgin hemlock* (fig. 4).—Size 12 acres, located four miles east of Highlands on Route 64, opposite plot 1. This plot is owned and preserved by Mr. Henry Wright and is a remnant of the once extensive virgin hemlock forest known as the "Primeval Forest" or "Ravenel's Woods." Hemlock, with trees 3 to 4 feet in diameter and 400 years or more old, comprise ¾ of the stand by basal area.

FIG. 4. Interior of the virgin hemlock forest with dense understory of Rhododendron.

Black birch, many reaching very large size, red maple, Frazier's magnolia, red oak, and other deciduous trees are widely scattered in the stand. The understory over most of the area is a mass of *Rhododendron maximum,* often almost impenetrable. Oosting and Billings ('39) in their study of the "Primeval Forest" before its destruction found that hemlock was the chief dominant in all the vast area, but there were two distinct types based on the composition of the understory: *Rhododendron* type and *Polycodium* type, the latter having a greater percentage of deciduous elements and occurring on higher ground. The present study plot is typical of the *Rhododendron* type.

4. *Xeric shrubland* (fig. 5).—Size 4.3 acres, located on a hillside sloping up from Highway 64 three and a half miles east of Highlands. Vegetation is typical of that which follows, within a few years, the removal the oak-chestnut forest. Brambles (*Rubus*), black locust, sumac, and cherry are the most numerous species of shrubs and small trees which occur in dense thickets interspersed with more open places dominated by grasses and herbs.

5. *Intermediate (second growth) deciduous forest* (fig. 6).—Size 10 acres,

FIG. 5. Xeric shrubland which has followed the logging of the climax oak-chestnut forest. Black locust, brambles (*Rubus*), sumac, and a large chestnut stump with a few chestnut sprouts may be seen in the picture.

FIG. 6. Interior of the intermediate or second-growth deciduous forest. The study plot contains a few large trees but is largely covered with a dense stand of small trees and saplings.

FIG. 7. Interior of the mature oak-chestnut study area, showing large mature oaks and a fallen chestnut tree in foreground. In the background the death of a group of chestnuts (killed by chestnut bark fungus disease) has created a sun-lit, shrub-filled opening. This particular study plot, while modified by the chestnut blight in common with all the Appalachian oak-chestnut forests, has been little disturbed by man.

located on a steeply sloping hillside four and a half miles east of Highlands near plots 1 and 3. Vegetation consists of a rather uniform stand of oaks, hickories, maples and other deciduous trees 4–10 inches D.B.H. There is a well developed herb layer and less dense shrub layer. A few small hemlocks, a few chestnut sprouts, and one or two patches of *Rhododendron* occur. The plot is a good example of a young forest which has developed after the clear cutting of the original oak-chestnut forest on the mountain slope.

6. *Mature oak-chestnut (climax) forest* (fig. 7).—Size 25 acres, located on a steeply sloping hillside near plot 4, three and one-half miles east of Highlands. Vegetation is typical of the mature mountain slope forest relatively undisturbed by man. However, since all large chestnuts have been killed by the blight, openings have been created in the otherwise continuous canopy with the result that patches of young vegetation, along with vigorous chestnut sprouts, occur scattered throughout the stand. Shrub and herb layers are well developed. Hemlock and *Rhododendron,* which are so characteristic of the mesic forests, are of very minor importance on the plot.

RESULTS

Densities calculated in pairs per 100 acres for each of the six study areas are given in tables II and III. Except for plot 6, studied for one season only, figures represent averages of both the 1946 and 1947 census results, there being very little difference in the two years. In the two shrubland plots and the intermediate de-

ciduous forest area a 10% reduction was made to correct for small size of plot as previously explained. In the tables, the data are arranged so as to show successional changes occurring during the development of forest from shrubland stages in each of the two seres. These data clarify and make quantitative the relation between common breeding birds of the region and major plant communities, even though it should be emphasized that they do not give a complete picture of successional changes.

Total populations

The density of birds differs rather strikingly in the two community series. In the upland oak-chestnut sere, populations are high in the shrub stage and decrease as the forest matures, even though the chestnut blight has created considerable "edge effect" in the mature forest. In the hemlock sere, on the other hand, the high density in the shrub stage is maintained or even increased with the development of the climax. The greater density in forests of hemlock sere is correlated with (1)

TABLE II. *The hemlock sere*

	Pairs per 100 acres		
	Mesic shrubland (plot 1)	Intermediate hemlock-hardwood (plot 2)	Virgin hemlock (plot 3)
Song Sparrow (*Melospiza melodia*)	126	—	—
Chestnut-sided Warbler (*Dendroica pensylvanica*)	49		
Catbird (*Dumatella carolinensis*)	42	25	16
Field Sparrow (*Spizella pusilla*)	22		
Towhee (*Pipilo erythrophthalmus*)	14		
Goldfinch (*Spinus tristis*)	14		
Brown Thrasher (*Toxostoma rufum*)	14		
Indigo Bunting (*Passerina cyanea*)	7		
Wood Thrush (*Hylocichla mustelina*)		42	10
Black-throated Blue Warbler (*Dendroica caerulescens*)		40	75
Blue-headed Vireo (*Vireo solitarius*)		30	25
Black-and-white Warbler (*Mniotilta varia*)		27	12
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)		17	2
Blackburnian Warbler (*Dendroica fusca*)		10	49
Flicker (*Colaptes auratus*)		10	—
Red-breasted Nuthatch (*Sitta canadensis*)		8	17
Junco (*Junco hyemalis*)		8	—
Veery (*Hylocichla fuscescens*)		8	—
Wood Pewee (*Contopus virens*)		8	6
Scarlet Tanager (*Piranga olivacea*)		7	27
Cedar Waxwing (*Bombycilla cedrorum*)		7	—
Ovenbird (*Seiurus aurocapillus*)		5	—
Carolina Chickadee (*Parus carolinensis*)		5	8
Red-eyed Vireo (*Vireo olivaceus*)		3	—
Cardinal (*Richmondena cardinalis*)		3	—
Parula Warbler (*Parula americana*)		3	17
Hooded Warbler (*Wilsonia citrina*)		2	—
Robin (*Turdus migratorius*)		2	—
Canada Warbler (*Wilsonia canadensis*)			33
Hairy Woodpecker (*Dendrocopus villosus*)			10
Brown Creeper (*Certhia familiaris*)			8
White-breasted Nuthatch (*Sitta carolinensis*)			8
Crested Flycatcher (*Myiarchus crinitus*)			4
Tufted Tutmouse (*Parus bicolor*)			2
Broad-winged Hawk (*Buteo platypterus*)			2
Totals	288	270	331

TABLE III. *The oak-chestnut sere*

	Pairs per 100 acres		
	Xeric shrubland (plot 4)	Intermediate deciduous forest (plot 5)	Mature climax* (plot 6)
Chestnut-sided Warbler (*Dendroica pensylvanica*)	108	—	8
Towhee (*Pipilo erythrophthalmus*)	108	—	6
Catbird (*Dumatella carolinensis*)	68	—	—
Field Sparrow (*Spizella pusilla*)	45	—	—
Golden-winged Warbler (*Vermivora chrysoptera*)	18	—	—
Brown Thrasher (*Toxostoma rufum*)	18	—	—
Indigo Bunting (*Passerina cyanea*)	18	—	—
Goldfinch (*Spinus tristis*)	9	—	—
Flicker (*Colaptes auratus*)	4	—	—
Ovenbird (*Seiurus aurocapillus*)		50	38
Red-eyed Vireo (*Vireo olivaceus*)		45	12
Blue-headed Vireo (*Vireo solitarius*)		38	22
Black-throated Blue Warbler (*Dendroica caerulescens*)		23	24
Black-and-white Warbler (*Mniotilta varia*)		15	4
Wood Pewee (*Contropus virens*)		15	2
Scarlet Tanager (*Piranga olivaceus*)		15	—
Wood Thrush (*Hylocichla mustelina*)		8	8
Robin (*Turdus migratorius*)		8	2
Downy Woodpecker (*Dendrocopus pubescens*)		2	4
Hairy Woodpecker (*Dendrocopus villosus*)		2	4
Carolina Chickadee (*Parus carolinensis*)		1	2
Veery (*Hylocichla fuscescens*)			12
White-breasted Nuthatch (*Sitta carolinensis*)			4
Ruby-throated Hummingbird (*Archilochus colubris*)			4
Tufted Titmouse (*Parus bicolor*)			2
Ruffed Grouse (*Bonasa umbellus*)			2
Totals	396	222	160

* Modified by chestnut blight, see text.

greater moisture content and (2) presence of both coniferous and deciduous life forms. How these factors may influence the bird population will be discussed later in this paper.

Species differences

Species composition of comparable communities in the two seres was not greatly different, there being very few species that nest exclusively in only one sere, but the relative abundance and consequent importance of many species was found to be different in the two community series. In other words, the two seres appear to differ quantitatively much more than qualitatively.

Observation in the region as a whole has indicated that red-breasted nuthatch, brown creeper, blackburnian warbler, and perhaps parula warbler and song sparrow nest entirely or very largely in the moist communities of the hemlock sere. All other common species of hemlock sere have been found at least sparingly in the oak-chestnut series even though not all were necessarily recorded in the small sample areas actually censused. Conversely, the xeric communities apparently have no exclusive species.

While it is thus difficult to find species differences in the two seres, the abundance of many species proved to be quite different. The Cairns's or mountain subspecies of the black-throated blue warbler (*Dendroica coerulescens cairnsi*) ranked near the top in forest stages of both seres, the density, however, being greater in the

forest stages of the hemlock sere, averaging 57 pairs per 100 acres for the two forest plots of the former and about 24 pairs per 100 acres for comparable stages in the oak-chestnut series. These measurements provide definite statistics to support the impression which one gets from general observation in the region, namely, that the Cairns's warbler is the most abundant forest bird of the region. The solitary or mountain subspecies of the blue-headed vireo (*Vireo solitarius alticola*) was one of the few species which showed the same abundance in the two seres, averaging 28 and 30 pairs per 100 acres, respectively. This species probably can be considered the second most common bird of forests in general, although it is outranked in one or other of the seres by several species.

In contrast to the blue-headed vireo, the blackburnian and Canada warblers showed a high abundance in hemlock forests and were absent in the xeric communities . Conversely, the ovenbird and red-eyed vireo were very important members of the oak-chestnut forests and of minor importance in the hemlock-hardwood forests. These four species were responsible for a large part of the difference in bird populations of the forest stages of the two community series.

In the shrubland communities, the chestnut-sided warbler was very abundant in both seres, and, with an average abundance of 79 pairs per 100 acres, can be rated the most abundant species of the early stages of succession generally. The greatest difference in the two seres at the shrubland stage resulted from the fact that the song sparrow was prominent in the mesic community and the towhee correspondingly abundant in the xeric community, these two species being responsible for most of the difference in the two populations (see tables II and III).

Comparison of study plots by means of percentage differences

In addition to revealing specific differences and similarities in populations of different areas, as had been done in the preceeding paragraphs, some statistical means of comparing the *total* population, including species composition and density as well as total density, would be desirable. While the methods and results of field censuses are not yet precise enough, nor the variables sufficiently well known to warrant refined statistical analysis, percentage comparisons would seem to be justified, as an aid, at least, in comparing one community with another. In table IV each of the six plots is compared with every other one by means of "percentage differences." These percentages are calculated as follows: The difference in density (in pairs per 100 acres) for each species occupying the two areas being compared is determined. Thus, if species

TABLE IV. *Percentage difference in the breeding bird population of the six study plots compared with each other*

	Mesic Shrubland (plot 1)				
Intermediate Hemlock (plot 2)	95.8	Intermediate Hemlock (plot 2)			
Virgin Hemlock (plot 3)	97.9	50.5	Virgin Hemlock (plot 3)		
Xeric Shrubland (plot 4)	51.8	95.6	97.8	Xeric Shrubland (plot 4)	
Intermediate Oak-chestnut (plot 5)	100.0	60.9	65.5	100.0	Intermediate Oak-chestnut (plot 5)
Mature Oak-chestnut (plot 6)	93.8	63.7	68.6	96.9	39.6

one has 20 pairs in plot A and 10 in plot B, the difference is 10 pairs; or if species B has 10 pairs in plot A and none in plot B the difference is also 10 pairs. All these differences are then added and the total divided by the total number of pairs on both areas to determine the percentage difference between the two populations. The procedure is worked out in detail in table V. This "percentage difference" (or its complement "percentage similarity") thus is a rough index of difference (or similarity) in species composition and in density, the commonest species having the greatest weight in determination of the figure. A percentage difference of 100 indicates that the populations of the areas being compared are entirely different, with no species in common. A figure of less than 50% indicates a close similarity in two populations. Since even plots of the same community side by side

TABLE V. *Breeding bird population of Highlands, North Carolina, hemlock-hardwood forest (A) compared with West Virginia spruce-hardwood (B), and New York hemlock-beech (C)*

	A	B	Diff. A-B	C	Diff. A-C	Diff. B-C
Black-throated Blue Warbler*	57	16	41	9	48	7
Blackburnian Warbler	30	55	25	14	16	41
Blue-headed Vireo	28	26	2	1	27	25
Wood Thrush	26	3	23	1	25	2
Black and White Warbler	20	—	20	2	18	2
Catbird	20	—	20	—	20	0
Canada Warbler	16	16	0	10	6	6
Scarlet Tanager	17	7	10	5	12	2
Parula Warbler	10	3	7	—	10	3
Rose-breasted Grosbeak	10	3	7	—	10	3
Red-breasted Nuthatch	12	7	5	—	12	7
Chickadee (Carolina or Black-cap)	6	2	4	9	3	7
Wood Pewee	7	—	7	—	7	0
Hairy Woodpecker	5	3	2	3	2	0
Flicker	5	—	5	—	5	0
Brown Creeper	4	7	3	—	4	7
White-breasted Nuthatch	4	—	4	5	1	5
Junco	4	21	17	—	4	21
Veery	4	7	3	5	1	2
Ovenbird	2	3	1	32	30	29
Crested Flycatcher	2	—	2	1	1	1
Red-eyed Vireo	2	10	8	1	1	9
Robin	1	3	2	—	1	3
Hooded Warbler	1	—	1	—	1	0
Cardinal	1	—	1	—	1	0
Tufted Titmouse	1	—	1	—	1	0
Blue Jay	1	3	2	2	1	1
Magnolia Warbler (*Dendroica magnolia*)		45	45	25	25	20
Golden-crowned Kinglet (*Regulus satrapa*)		32	32	—	—	32
Black-throated Green Warbler (*D. virens*)		31	31	32	32	1
Olive-backed Thrush (*Hylocichla ustulata*)		13	13	—	—	13
Hermit Thrush (*Hylocichla guttata*)		3	3	6	6	3
Winter Wren (*Troglodytes troglodytes*)		3	3	—	—	3
Purple Finch (*Carpodacus purpureus*)		3	3	—	—	3
	296	325	353	163	331	258

Percentage diff. A-B $\frac{\text{AB diff. } 353}{\text{A + B } 621} = 56.8.$

Percentage diff. A-C $\frac{\text{AC diff. } 331}{\text{A + C } 459} = 72.1.$

Percentage diff. B-C $\frac{\text{BC diff. } 258}{\text{B + C } 488} = 52.9.$

* For scientific names see table II.

would show at least small differences, a figure of zero would probably not be obtained in actual practice.

In table IV it will be seen that populations of the shrubland areas show a 94 to 100% difference from forest plots in either or both seres, a reflection of the fundamental importance of vegetational life-form. The two plots which are most alike are the second-growth and the mature oak-chestnut with a 39.6 percentage difference. This small difference in avifauna is clearly correlated with the results of chestnut blight which has "opened up" the mature stand until it resembles a younger forest, or even a shrubland, into which chestnut-sided warblers and towhees, birds of early seral stages, have reinvaded. Eventually, the openings created by death of the chestnuts will be filled, but for the time being the vigor of the chestnut sprouts produces a sort of shrub disclimax (see Odum and Burleigh, '46) within the forest. The bird population reflects very well the mixture of open shrub and closed forest vegetation and illustrates how well birds may serve as indicators to ecological conditions and changes.

When similar stages in the two seres are compared a gradual divergence in bird population is indicated, that is, mature communities differ from each other more than the young communities. Thus, the percentage difference between the two shrubland stages is 51.8, between the two young forests 60.9 and between the mature stages 68.6. The latter figure might possibly be somewhat different without the disturbing influence of the chestnut blight.

Comparison with other Appalachian regions

In table V the bird population of the hemlock-northern hardwood forest on the Highlands Plateau (column A) is compared with the population of a spruce-northern hardwood forest in the Cheat Mountains of West Virginia (column B) censused by Stewart and Aldrich ('49) and the population of a hemlock-beech forest on the Helderberg Plateau of east-central New York (column C) censused by Kendeigh ('46). In column A, the virgin and the intermediate plots at Highlands are combined to give an average picture of the hemlock-hardwood forest and to make the total sample (27 acres) similar in size to that in the other studies. Hawks, owls, the pileated woodpecker and the ruffed grouse are omitted from the tabulation since none of the study plots are large enough adequately to census these large birds.

All three of these localities lie in the ecotone between the Northern Coniferous Forest (or Taiga) Biome and the Eastern Deciduous Forest Biome, the plant community of the West Virginia mountains being more closely allied floristically to the Northern Coniferous Forest. Average summer temperatures are about the same for the three regions but rainfall is much heavier in the southern Appalachians as shown by the following data: [2]

	Average temperature, ° F.		Total annual precipitation, inches
	Jan.	July	
Highlands, N. C.	39.7	70.5	82.6
Cheat Mts., W. Va.	30.9	68.6	68.7
Helderberg Pl., N. Y.	22.3	68.6	34.9

Referring to table V, it will be noted, first, that the total population density of the North Carolina and West Virginia plots is similar and both have nearly twice as many birds as the New York plot. This is correlated with the higher rainfall and the greater development and diversification of the forest understory in the two southern regions, the New York forest being rather open with scant under-

[2] Data taken from U. S. Dept. Agriculture Yearbook of 1941, *Climate and Man.* Weather stations at Highlands and West Berne, N. Y., are close to study areas. For Cheat Mountains, the Pickens (Randolph County) data are used, which according to Maurice Brooks (personal communication) may be considered average for the higher altitude regions.

growth. This difference in the understory is a regional one, and not just local. For example, Brooks ('43) states that "in the southern Appalachians the development of a rich and varied shrub understory . . . is, perhaps, the most prominent characteristic of the vegetation" and serves to distinguish these mountain forests from similar ones farther north.

As shown by the percentage-difference figures, species composition in the three plots is remarkably similar, considering the great distance separating them. Thus, the North Carolina hemlock-hardwood forest and West Virginia spruce-hardwood forest showed only a 56.8 per cent difference, and the West Virginia forest was likewise not greatly different from the New York hemlock-hardwood forest (52.9%). The extremes in the series, the North Carolina and the New York plots, geographically the farthest apart, showed a greater percentage difference (72.1%), as might be expected.

In general, five or six species are chiefly responsible for the north-south difference in Appalachian coniferous-hardwood forests, as far as the sample plots are concerned. The Highlands plot lacks three species that are very important in the areas to the north, namely, golden-crowned kinglet and magnolia and black-throated green warblers. Highlands is south of the range of the magnolia warbler and virtually south of the range of the golden-crowned kinglet. The latter has been reported from the Highlands region in summer by T. D. Burleigh and A. H. Howell (Stevenson, '41) and may breed there rarely, but I was unable to find it in the course of the present study. On the other hand, the range of the black-throated green warbler continues into Georgia and Alabama, far south of Highlands; hence its absence on the Highlands Plateau is puzzling. A few individuals of this species appear in mid- or late summer, but I found no evidence that the species breeds anywhere in the area in any kind of habitat, this being also the experience of previous observers in the region (Stevenson '41). Southwest of Highlands in Gilmer and Pickens County, Georgia, the species is a locally common breeding bird. In this region, as elsewhere in the southern Appalachians, it has become adapted to deciduous forests, especially those with a mixture of Virginia or scrub pine (*Pinus virgianana*), and often breeds at low altitudes (Odum, '45); where available, it also occupies hemlock or hemlock-white pine stands along with the blackburnian warbler, its common associate in the north. The best explanation for the absence of the black-throated green warbler at Highlands seems to lie in the historical factor rather than any climatic or habitat limiting factors. The southern part of the range of this bird is "split" or bifurcate. There is a coastal population, *Dendroica virens waynei* breeding south to South Carolina and a mountain population, *D. v. virens* breeding south to Alabama, with an area in between not occupied by either race. Apparently, the high plateau on which Highlands is located and the adjacent areas in northeast Georgia have been bypassed and not yet occupied by the mountain race which is common to the west. Recently, the birds breeding in western South Carolina have been referred to the coastal race, *waynei* (see Sprunt and Chamberlain, '49). If this is verified by further taxonomic study, then Highlands would appear to be located in the hiatus between the two populations. In the forests of Highlands Plateau the particular niche of the black-throated green, the medium level stratum, is apparently not occupied by any other warbler or species with similar ecological requirements. If the black-throated green warbler were present in numbers, say, 30 pairs per hundred acres, the percentage difference between the Highlands study areas and those further north would be greatly reduced.

Looking at table V from the other view, that is, species present in the southern end of the Appalachian chain but not present in the northern portion, we find

that no species of primarily southern distribution (for example, hooded warbler) figured prominently in the population of the hemlock-hardwood forest; rather, the black-throated blue warbler, wood thrush, black and white warbler, and catbird, all of which breed throughout the Appalachian region, were more abundant in the southern end and largely compensated for the absence of the three species mentioned above. The greater abundance of the black-throated blue warbler in the central and especially in the southern Appalachians seems well correlated with the rich development of the shrub understory (as previously described) which provides its particular niche within the forest. The Appalachian subspecies, *cairnsi,* is especially associated with (but not restricted to) *Rhododendron,* a characteristic shrub constituent not only of the mixed forest but the moister portions of the oak-chestnut and other deciduous forests as well.

The catbird, generally considered a bird of the forest edge or early seral stages, was not restricted to these habitats at Highlands, but occupied *Rhododendron* thickets at some distance from the forest edge wherever there was a small opening in the canopy left by a fallen tree. This species, incidentally, was the only one occurring in all three stages of succession in the hemlock sere (table II).

While the birds of the hemlock-hardwood forests at Highlands have thus been shown to be closely allied both qualitatively and quantitatively to those of more northern forests in the coniferous-deciduous forest ecotone, the population of the Highlands oak-chestnut forests, although representing a mature climax community growing at the same or greater altitude, appears to be more closely related to forest populations of Eastern Deciduous Forest Biome. Thus, the ovenbird and red-eyed vireo, among the four most abundant species at Highlands, rank as the two most abundant species in a series of eight mature deciduous forests located in Virginia, West Virginia, New York, and Ohio as summarized by Kendeigh ('44, table 20). Likewise, general species composition is similar. As far as birds are concerned, therefore, the classification of the oak-chestnut association as a sub-division of the Eastern Deciduous Forest Biome seems justified. The oak-hickory climax forest of the piedmont plateau of North Carolina and Georgia, as censused at Chapel Hill (H. T. Odum, '46) and Athens (E. P. Odum, '47), differs chiefly from the southern Appalachian oak-chestnut forest in having (1) fewer or no ovenbirds, (2) more wood thrushes, (3) the summer tanager replacing the scarlet tanager, (4) hooded warblers, yellow-throated vireos, and Carolina wrens in moderate numbers, and (5) no black-throated blue warblers, veerys, or blue-headed vireos (see, however, subsequent discussion of recent invasion of latter species into the piedmont). Otherwise, there are many similarities, including the fact that the red-eyed vireo ranks first or second in abundance in both regions. Detailed percentage analyses and a more precise evaluation of the ecological relations of the bird populations of the mountain deciduous forests must await the gathering of additional quantitative data from the southeastern region generally.

Discussion

Population density and plant succession

In his pioneer study of the "ecological succession of birds" on Isle Royale, C. C. Adams ('08) stated that as far as the number of species occupying successive vegetative stages was concerned, there was a "development of diversity from simplicity and a later return to simplicity." Population density seems often to show a similar trend, especially in secondary seres on the upland, in which a peak in population is reached somewhere in the middle of the successional series.

On the Highlands Plateau bird population density in the oak-chestnut sere followed the trend indicated in the pre-

vious paragraph. Very early vegetation stages, or grassland communities, developing on cleared land are but poorly developed at high altitudes and were not censused in this study, but were observed to be thinly occupied by birds. Typical grassland species of lower altitudes and the piedmont region (meadowlark and grasshopper sparrow, for example) are largely absent from Highlands. When the development of the vegetation reaches the shrub and young forest stages, the communities are well occupied by birds, and, as already indicated, population density decreases as the forest matures, even with disturbing influence of the chestnut blight.

In the hemlock sere, on the other hand, this "typical" population density-succession curve is modified, since the high populations of shrubland stages are maintained or increased as the forest matures, even including very old virgin tracts. Moisture may be the key to this difference. So much emphasis has been placed on temperature as a factor controlling distribution and abundance of birds, that the importance of the water factor has often been overlooked. Since Highlands is near the center of an area which has the highest annual rainfall in the eastern United States (80 inches or more as previously indicated), moisture is an especially important ecological factor. The high water content of the forests of the hemlock sere could conceivably result in increased populations both directly by providing more available water and by moderating temperature changes, and indirectly by producing a more luxuriant vegetation with consequent greater variety of niches and, perhaps, a greater amount of food. At present, there is no way to evaluate accurately the importance of these possibilities.

Comparison with adjacent biotic regions

Following Stewart and Aldrich's census of the West Virginia spruce-hardwood forest in 1947 (Stewart and Aldrich, '49) DeGarmo repeated the study on the same area in 1948 (DeGarmo, '48). He found the population to be very similar to that of the previous year (as shown in Table V), but the total density was even greater —381 pairs per 100 acres. This two-year coverage by different observers plus our two year coverage of two different plots at Highlands seems to indicate that the high population density reported for these areas was not temporary or local in nature only. Thus, it can be tentatively concluded that the bird population density of the mixed coniferous-hardwood forests of the southern Appalachians is very high for forest communities, higher than has been generally reported for climax forests in the adjacent Deciduous Forest Biome. Thus, Kendeigh ('44) reports that the average density for 8 climax deciduous forest communities scattered widely over eastern North America is 221 pairs per 100 acres as compared with 300 or over for the Appalachian area. On the Georgia piedmont, 100 miles south of Highlands, our two-year study of an oak-hickory climax forest yielded an average of 225 pairs per 100 acres. The question then arises as to whether the higher density is due to high rainfall as previously discussed, or partly, at least, to the mixed composition of the forest, a sort of "ecotone" or "edge effect," as it were. In other words, the mixed forest provides habitat both for species adapted to coniferous and deciduous life-forms and thus the forest as a whole might support a greater population than pure stands of either. In this connection, the comparison between the New York beech-hemlock forest and the Highlands hemlock-hardwood forest is of interest (table V). Both forests are mixed and both have about the same two to one dominance of hemlock, yet Highlands' forests, located in a region of greater rainfall and having a more luxuriant understory, have twice as large a bird population (as is also true of the West Virginia plot). The results of the annual breeding-bird censuses in Audubon Field Notes provide further evidence that moist communities support high

populations since swamp, bog, floodplain, and coastal hammock forests as well as marshes consistently show high densities.

Another factor that should not be overlooked is a historical one which has been advanced by Brooks ('47), who suggests that during glacial times northern birds were crowded into the unglaciated southern Appalachians where they were forced to seek out all possible niches in order to survive, thus explaining the diverse and atypical habitat choice of some species. This might also be a factor in the present high population density although it would seem that it would have more influence on the richness of the avifauna rather than on the number of individuals; the latter would more likely be controlled by the present day carrying capacity of the habitat. Actually, however, all of the suggestions in this section can only be considered as suggestions; what is needed are more data, especially more comparative analyses of populations of different communities and regions.

Population density and avian invasion

During the past forty years, at least four species of birds, the robin, song sparrow, chestnut-sided warbler and blue-headed vireo, have made rather rapid and spectacular extensions of range in the southern Appalachian region (Odum and Burleigh, '45; Odum, '48). The robin, song sparrow and blue-headed vireo have invaded the piedmont region from the mountains, the latter two having only barely entered this region during the past 5 to 10 years. The chestnut-sided warbler has extended its breeding range to the end of the main Blue Ridge (Pickens County, Georgia) which was not occupied prior to 1910. These invasions seem to have resulted from wholesale habitat changes by man and the chestnut blight, but as was pointed out in a previous paper (Odum and Burleigh, '46) a build-up in population, or some degree of population pressure, might be expected to occur before a species, otherwise able to breed in new territory, would actually invade it. The present study provides some evidence to support this contention, since the song sparrow, chestnut-sided warbler, and blue-headed vireo proved to be extremely abundant birds in the sample areas of their habitat located in the general region from which invasion of the Piedmont or more southern mountain areas must have been launched. The robin's forest-edge habitat was not sampled in this study, but there can be little doubt that this species also became very abundant within its range prior to and during the southward range extension. It should be emphasized that, as here conceived, some degree of population pressure might precede or accompany an invasion of new territory, but in itself does not necessarily *cause* an invasion; thus, many other species are abundant in the region in question, the black-throated blue warbler, for example, but have shown no recent invasion tendencies. Climate or habitat limiting factors in most cases presumably prevent an extension of the range even when a species becomes very successful within its original range.

Summary

1. Breeding bird populations were measured on six plots representing shrubland, intermediate forest, and mature or climax forest stages in each of two community series, the hemlock and the oak-chestnut seres, located on the Highlands Plateau, a high altitude region on the main Blue Ridge of the Appalachian mountains located where North Carolina joins Georgia and South Carolina. All plots were between 3,800 and 4,100 ft. altitude and, with one exception, were censused for two consecutive breeding seasons (1946, 1947) by the use of the "spot-mapping" or "territory mapping" method. In size, plots ranged from 4.6 to 25 acres. Density calculations on plots 10 acres or less were corrected to compensate for small size of sample (table I). Data were tabulated to show successional trends in the two seres (tables II and III).

2. Population density was high in the shrubland stages of both seres (288 and 396 pairs per 100 acres). In the oak-chestnut series density was less in the forest stages (222 and 160 pairs per 100 acres, table III), while in hemlock sere high populations were maintained or were increased in the mature stages (270 and 331 pairs per 100 acres, table II).

3. In species composition, communities of the two seres were similar, only a few species (red-breasted nuthatch, and brown creeper, for example) being restricted to communities in the moist series. The abundance of many species differed greatly, however. In the forest stages, the black-throated blue, blackburnian, and Canada warbler were much more abundant in the hemlock sere and red-eyed vireo and ovenbird were much more abundant in the oak-chestnut sere. The blue-headed vireo showed an approximately equal abundance in both. In the shrubland stages the chestnut-sided warbler was abundant in both, but the song sparrow was abundant in and restricted to the mesic shrubland and the towhee more abundant in the xeric shrubland.

4. The total populations of all six plots were compared with each other by means of "percentage differences" (table IV). Populations of the mature forest communities in the two seres showed a greater percentage difference (68.6) than did the two shrubland communities (51.8%). Shrubland communities in general showed a 93.8 to 100 per cent difference from forest communities. The two plots which were least different in bird population were the intermediate and mature forests of the oak-chestnut series (39.6 percentage difference), this being correlated with the effect of the chestnut blight which has created openings and patches of younger vegetation in the mature forest into which species of earlier seral stages have re-invaded.

5. The population of the Highlands hemlock-northern hardwood forest (intermediate and virgin plots combined) is compared with a spruce-hardwood forest in West Virginia and a hemlock-beech forest on Helderberg Plateau of New York (table V). In species composition the three areas were remarkably similar, only 7 species found in one or the other of the northern areas being absent at Highlands. The density of many species was also similar, but in other species there were important differences. The magnolia warbler, golden-crowned kinglet and black-throated green warbler were important constituents of the population of one or both of the more northern plots and absent (possibly very rare in the case of the kinglet) at Highlands. The black-throated blue warbler, wood thrush, black-and-white warbler and several others, although present in the northern areas, were much more abundant at the southern end of the Appalachian chain. Percentage difference for total populations between N. C. and W. Va. plots was 56.8, between W. Va. and N. Y., 52.9, and between N. C. and N. Y., 72.1.

6. Since the black-throated green warbler breeds much farther south and at lower altitudes than Highlands, it is concluded that its absence in the region is due to a historical factor rather than to any climate or habitat limiting factor. It is suggested that the Highlands Plateau may have been by-passed and not yet occupied and may now be a part of a hiatus between breeding ranges of the two races, *D. v. virens* and *D. v. waynei.*

7. Greater moisture and greater development of the forest shrub understory are believed to be the key factors which produce the higher populations found in the mature forests of the hemlock sere as compared with the comparable stages of the oak-chestnut sere. Likewise, higher rainfall and greater understory development in the southern Appalachians generally are correlated with the fact that both Highlands and the West Virginia coniferous-hardwood forest had higher populations than the New York mixed forest or climax deciduous forests as reported in the literature. Mixed life form and post-glacial history are also discussed as pos-

sible factors contributing to high forest populations.

8. The census results provided some evidence to support the contention mentioned in a previous paper (Odum and Burleigh, '46), that a build up in population, or some "population pressure," may precede or accompany (although not necessarily cause) the extension of a bird species' breeding range. Three species, the song sparrow, blue-headed vireo, and chestnut-sided warbler, which are now known to be actively invading the lower mountain regions and the piedmont plateau (in case of the former two), proved to be extremely abundant birds on the Highlands Plateau.

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VEGETATION AND SOIL PROFILES IN SOME SOLIFLUCTION AND MOUND AREAS IN ALASKA

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INTRODUCTION

During the summer of 1949 while investigating grasslands and other types of vegetation in Alaska, opportunities became available to compare a number of solifluction and non-solifluction areas. The main areas studied (see map, fig. 1) were located on Eagle Summit (station E) on the Steese Highway between Fairbanks and Circle Hot Springs, in Mount McKinley National Park (station M), near Healy (station H), in the Craigie Creek Valley (station C) in the Talkeetna Mountains, and in the vicinity of Kotzebue (station K). Solifluction is widespread in the mountains in various parts of Alaska (Cairnes '12, Capps '13, '40, Eakin '16, Leffingwell '15, '19, Mertie '17, Sharp '42, Smith '10, '17, Taber '43), but little information is available concerning the vegetation of solifluction areas. The purpose of the present paper is to point out some relationships between the vegetation, the soil profile, and solifluction in Alaska.

The term "solifluction" was proposed by Andersson ('06) for the slow flowing from higher to lower elevations upon frozen ground (*"tjäle"*) of masses of soil material saturated with water. Salomon-Calvi ('29) attempted to restrict the use of this term to movement upon permanently frozen ground, but in general usage it has come to mean the fluid-like movement of ground materials upon a sloping, impermeable basal surface such as frozen ground or rock, and is not confined to flow under conditions of freezing and thawing. Sørensen ('35) described four ground layers occurring in solifluction land: 1) the basal impermeable surface, which may be frozen ground (*"tjäle"*), causing concentration of water above it; 2) a thin, water-saturated flowing layer of silt or clay (*"leichtfliessende Fliesserdemasse"*) upon the impermeable layer, an essential layer for movement; 3) upon this a firmer layer of silt or clay, with water-filled pores, *"besitzt 'Tragvermögen,'"* also essential for movement; and 4) a non-flowing, firm, more or less crust-like layer on the surface, often drier than the horizons below and may be lacking entirely. Bryan ('46) suggested the term "congeliturbation" to include "solifluction" in Andersson's meaning, and defined by Bryan as "frost action including frost heaving and

FIG. 1. Map of Alaska showing location of stands. C, Craigie Creek stand in the Talkeetna Mts.; M, McKinley Park Stands; H, Healy; E, Eagle Summit; K, Kotzebue.

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differential and mass movements." Troll ('44) named movement in a definite direction, caused by pressure and having a leveling effect (*"fläckenhaft"*) as *"Hang-Solifluction";* and movement from the center of frost-caused structures to the periphery as *"Mikro-Solifluction."* Factors influencing solifluction and frost-heaving have been listed as: 1) the action of freezing accompanied by volume changes in forming a silt or clay layer upon a permanent or temporary frozen layer, 2) sufficient water to saturate at least a portion of this silt layer, 3) silt or clay particles of such a nature that they have the capacity to flow when sufficiently wet, 4) simple temperature changes, causing convection movements in materials of different specific gravity, 5) cohesiveness of freezing water, the upward movement of nonfrozen water from below, and the dispersal of clay particles which would facilitate movement, 6) degree of slope, 7) depth of the thawed ground (Sørensen '35, Troll '44).

On the basis of extensive investigations in Alaska, from the geological view-point, Taber ('43) made the following illuminating statements. "Gullying and slope wash from rain and melt water are entirely absent over much of the frozen ground area because of the dense blanket of peat and vegetation. . . . On perennially frozen ground, were slope wash is absent or reduced to a minimum, mass movements of soil become relatively more important. Coarse debris at the foot of cliffs and steep slopes moves downslope toward the streams, disintegrating in transit to finer material. The results of talus creep are similar in cold and temperate regions, but, as the debris becomes finer, differences become more noticeable, and certain features that develop, such as stone polygons or polygonal nets, stone stripes, altiplanation terraces, turf-banked detritus benches, and some kinds of mud flow, are largely if not entirely limited to perennially frozen ground. . . . Solifluction is interpreted by most writers as a movement faster than creep. . . . Freezing and thawing and excessive water are, therefore, the major factors causing mass movements of soil in cold climates."

Numerous papers (three late ones containing extensive bibliographies, Troll '44, Taber '43, Johnson '48) have been written on the ground aspects of solifluction (Beskow '30, '35, Paterson '40, Muller '47, Troll '47, etc.), but the vegetational aspects have received much less attention. Frödin's ('18) treatment of the relationship of the vegetation to solifluction in the alpine region of Swedish Lappland is outstanding. He distinguished the following main kinds of solifluction (*"Erdfliessen"*). 1) Mud- or siltflow (*"Schlammstrom"*), located nearest permanent snow fields and in which the movement is relatively rapid, usually lacks vegetation. 2) Glacier-like flows (*"Gletscher-fliesserde"*), the lower parts of the Schlammströme, are often in tongue-like, parallel streaks or stripes due to the more rapid movement of the silt in the center than in the borders. The vegetation often consists largely of small waves of liverworts, especially *Anthelia nivalis;* and other plants may also be present on these stripes, such as *Polytrichum* spp., various kinds of lichens, particularly *Solorina crocea,* and a few phanerograms such as *Salix herbacea* and *S. polaris.* Other species listed were *Lycopodium selago, Luzula confusa,* and the lichens *Alectoria ochroleuca, A. divergens, Sphaerophorus coralloides, Stereocaulon tomentosum,* and *S. paschale.* According to Frödin these plants offer some resistance to the flow of the entire earth mass. 3) Terrace solifluction (*"Fliesserdeterrassen"*), in which the earth flow (*"Erdstrom"*) is more uneven because of obstacles encountered causing terraces with usually steep escarpments to develop. In a large number of papers the vegetation is discussed, but little detail is given (Summerhayes and Elton '23, '28, Sørensen '35, Seidenfaden '31, Troll '44, Russell and Wellington '40, Taber '43, Gjaerevoll '49, and others). In a paper on the vegetation of East Greenland and Jan Mayen, Oosting ('48)

stated that "the developmental history of almost all the plant communities is at some time affected by solifluction. The species growing on moving soil must have some special adaptations which permit their survival, but the special features are not understood. Perhaps survival is possible because of interrelationships within the community. Certainly our knowledge of plant-solifluction relationships is not yet complete."

Procedure and Methods

Ernest Lepage, due to his long experience with the identification of Arctic and Subarctic plants, was able to name the species of most of the plants that were encountered. Herbarium specimens were collected of those about which the identification was doubtful and the aid of specialists in various groups of plants was secured, when necessary. The authority for each name used is given once in one of the tables, or in the text.

The point-contact method (Levy '27) was used to analyze the botanical composition of most of the stands which were studied. This method has been extensively tested and used (Hanson '50) to secure quantitative data on the degree of cover, or area occupied by plants, and the frequency (dispersion of the individuals of a species in the stand) of each species. The usual type of frame, holding 10 rods about ¼ inch in diameter and 2 feet long, inclined at a 45° angle, spaced 2 inches apart, was used. Records were kept of each time a plant, or part of a plant, of every species was touched by a rod. One rod might touch several leaves, flowers, or the stem of the same plant or of different plants in the same species, making a total, at times, of 10 or more hits for this one rod; or it might touch a plant only once, making only 1 hit. The first case would indicate much greater degree of cover than the second, but the frequency would be the same. The frame was set 20 times in each stand (making a total of 200 rod-contacts), spaced about 15 feet apart on 1 or 2 lines which were located in the well-developed portion of the stand, not too close to the boundaries. In the tables the total number of hits and the frequency of each species are shown. The relative area of bare ground is indicated by the number of "no hits," *i.e.*, the number of needles or rods which did not touch any plants. The greater the number of hits, or contacts, the greater is the degree of cover. The frequency is expressed in percentage, *e.g.*, if individuals of *Salix reticulata* in a certain stand were touched by 100 of the 200 rods the frequency would be 50 per cent. The range in frequency would therefore be from 0.5 per cent to 100.0 per cent. Usually there are only a few species that have high frequencies in a stand, showing a high degree of uniformity of distribution, and often indicating dominance. Most of the species have low frequencies, showing irregular or more scattered distribution.

In order to study the penetration of the roots and the soil profile, a trench, about 2.5 feet wide and 3 or more feet long, was dug to expose a vertical face of the substratum. The use of an ice-pick facilitated the detailed examination of the soil and the roots. Whenever possible the working depth (the depth to which a large number of roots penetrate and to which considerable absorption probably occurs) and the maximum depth (the deepest penetration of the roots) were determined. Often, however, these critical root-depths could not be determined because of water filling in the lower part of the trench too rapidly. In some of the stands the roots penetrated into the frozen ground and it appeared that the frozen portions of the roots might become active if the ground thawed. The color of the soil horizons was determined according to the standard color classification (Munsell '36) and samples which are used by the Soil Survey of the U. S. Department of Agriculture; the symbols which follow the color name in the detailed descriptions below refer to that classification. The author is indebted to Dr. C. E. Kellogg, Chief, U. S. Soil Survey, for suggestions in connec-

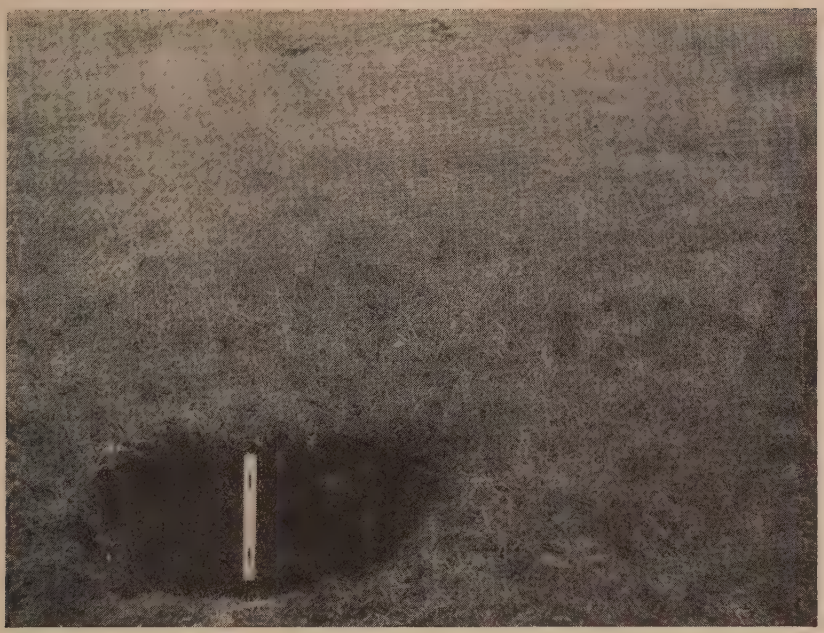

FIG. 2. Alpine Dryas-Sedge stand, Eagle Summit. Chief species are *Carex misandra, C. bigelowii, Dryas octopetala,* and *D. alaskensis.* West-facing slope of 5 to 10°. No frozen ground to depth of 36.5 inches. Ruler is one foot long. August 6, 1949.

tion with the study of soil profiles. The author is also indebted to various agencies in the U. S. Department of the Interior for assistance in a number of ways.

The present paper is not an exhaustive treatment, but the data and the suggestions offered should be helpful in further detailed studies conducted over a period of several years in restricted areas and with the use of permanent markers and study-plots.

STUDY AREAS

Eagle Summit, Steese Highway (Station E)

On August 6, 1949, two types of vegetation, "Alpine Sedge," "Alpine Dryas-Sedge" (Fig. 2), were studied on Eagle Summit, at an elevation of about 3,880 feet, the highest altitude reached on the Steese Highway between Fairbanks and Circle on the Yukon River. The latitude is about 65.5° N and the longitude about 145.5° W. These types occurred on moderate to steep slopes facing the west, north, or east usually. The particular stands studied were on westerly slopes of about 5° to 10°. The Alpine Sedge was saturated with water and solifluction was indicated by the hummocky surface and by terraces while the Alpine Dryas-Sedge stand (fig. 2) was only moderately moist and the absence of hummocks and terraces indicated that solifluction was not occurring. The vegetation in the former was very dense to a height of 5 or 6 inches and many of the leaves reached a height of 12 inches. In the latter a soft carpet-like growth of moss, about an inch thick, formed the ground-layer and the leaves of sedge and Dryas were usually not more than 3 to 5 inches tall, although some of the inflorescences of the sedges, poppy, and *Polygonum* extended to 8 to 15 inches. Analyses of these stands are shown in table I.

TABLE I. *Point-contact analyses of the Alpine Sedge stand (wet) and the Alpine Dryas-Sedge stand (moderately moist) on Eagle Summit*

Species	Alpine Sedge stand		Alpine Dryas-Sedge stand	
	Total hits	Freq., per cent	Total hits	Freq., per cent
Carex bigelowii Torr.	315	52.5	127	30.5
Carex membranacea Hook.	276	38.0	3	0.5
Carex vaginata Tausch.	18	4.0	5	1.5
Carex misandra R. Br.			138	34.0
Carex capillaris L.			23	5.5
Carex scirpoidea Michx.			4	1.0
Carex rupestris All.			1	0.5
Carex sp.			3	1.0
Eriophorum vaginatum L.	102	16.0		
Eriophorum angustifolium Roth.	30	12.5		
Dryas alaskensis A. E. Porsild	90	26.0	133	36.5
Dryas octopetala L.			136	26.5
Salix reticulata L.	13	6.5	2	1.0
Salix pulchra Cham.	7	1.0		
Salix arctica Pall.	5	2.0	16 ?	6.5
Vaccinium vitis-idea L.	13	5.0	6	2.5
Vaccinium uliginosum L.			29	10.5
Ledum decumbens (Ait.) Lodd.	5	1.5		
Poa arctica R. Br.	2	1.0	2	1.0
Hierochloa alpina (Sw.) Roem. and Schult.			5	2.5
Luzula confusa Lindeb.			6	1.5
Stellaria longipes Goldie	1	0.5		
Polygonum viviparum L.	7	3.0	8	3.5
Pedicularis capitata Adams.	1	0.5	3	1.0
Pedicularis langsdorfii Fisch.			5	2.0
Pyrola grandiflora Radius.	2	1.0		
Moss	140	70.0	Scattered	
Oxytropis scammaniana Hult.			23	6.0
Cassiope tetragona (L.) D. Don.			8	2.0
Eritrichium aretioides (Cham. and Schl.) DC.			8	2.0
Papaver macounii Greene			1	0.5
Dactylina arctica (Hook.) Nyl.			2	1.0
Cetraria sp.			1	0.5
Arctostaphylos alpina (L.) Spreng.			1	0.5
Saussurea angustifolia DC.			1	0.5
Silene acaulis L.			2	0.5
Arenaria rossii R. Br.			3	0.5
Tofieldia coccinea Richards			3	0.5
Rhododendron lapponicum (L.) Wahl.			1	0.5
No hits			3	1.5
Total number of hits	1029		712	
Additional species in stands but not hit				
Betula nana L. ssp. *exilis* (Sukatch.) Hult.	x			
Rubus chamaemorus L.	x			
Luzula multiflora (Retz.) Lej.			x	
Cardamine purpurea C. and S.			x	
Polygonum bistorta L. ssp. plumosum (Small) Hult.			x	
Eutrema edwardsii R. Br.			x	
Saxifraga punctata L.			x	
Tofieldia pusilla (Michx.) Pers.			x	
Empetrum nigrum L.			x	
Festuca brachyphylla Schult.			x	

Note: The most important species are given first except that species are placed in groups as sedges, grasses, forbs, heaths, mosses, lichens, as much as possible. Question mark indicates that plants could not be definitely identified.

In the Alpine Sedge stand a total of 19 species and a total of 1,029 hits were recorded; in the Alpine Dryas-Sedge stand 42 species and 712 hits. The latter stand offered a wider range of soil conditions than the former, which was evidently reflected in the number of species found in each. Due to the abundant and continuous supply of water in the former the cover was greater. The chief species in the Alpine Sedge stand were *Carex bigelowii, C. membranacea, Eriophorum vaginatum,* and mosses; in the Alpine Dryas-Sedge, *Carex misandra, Dryas octopetala, D. alaskensis,* and *Carex bigelowii.* As shown in the table more kinds of heath plants and many more species of forbs were found in the latter than in the former.

Alpine Sedge.—The characteristic features of the soil profile in the Alpine Sedge stand were: 1) the dark reddish brown layer of peat in the 0–7.5 inch horizon which was very distinct from the gray silt and gravel layer below; 2) the horizontal cleavage plane between the peat and the silt layer; 3) the abundance of roots to the depth of 24 inches; 4) scattered pools of water on the surface, water-saturated peat, and the poor drainage due to the compact silty layer at a depth of 7.5 to 10 inches; 5) frozen ground at 24 inches; 6) the very dark gray layer (frozen) beginning at 24 inches appeared to be a former surface horizon; 7) pH (as determined in the field by the use of the LaMotte-Morgan Soil Testing Set with bromcresol green, chlorphenol red, bromthymol blue, and phenol red indicator solutions) from 5.2 to 5.4 above the frozen ground, and 6.2 in the uppermost part of the frozen horizon.

Detailed description of the soil profile:

1–0 inch—dense layer of matted, partly decayed leaves, chiefly sedges.

0–7.5 inches—variable in thickness from 3.5 to 9.5 inches, mostly very dusky red (2/2–2/5YR), but in the lower half some portions are dark reddish brown (3/4–5YR), peat, roots very numerous, fibrous in structure, water-saturated, pH 5.4.

7.5–10.0 inches—gray (5/1–6/1–5Y), mottled with yellowish brown silt, containing many sand and small gravel particles, a compact, wet, fibrous horizon which tends to separate from the peat above by cleavage at its upper surface, roots very numerous, small rocks frequent, pH 5.2.

10.0–11.5 inches—transitional to the horizon below.

11.5–24.0 inches—gray to dark gray (5/1 to 4/1–5YR), mottled considerably with yellowish brown (5/6–10YR) especially in the lower part, silt similar to 7.5–10.0 inch layer but less compact and with higher content of sand and gravel particles, numerous stones, roots very numerous to 22 inches and then numerous to frozen ground at 24 inches, pH 5.2.

Below 24 inches—frozen, very dark gray (3/1–5YR), mottled with yellowish brown (5/4–10YR), silt with many sand and gravel particles, old roots frequent some of which appeared alive, stones frequent, this layer showed horizontal stratification, darker material appearing like decayed vegetation which gave this horizon the appearance of a former surface horizon, pH 6.2.

Alpine Dryas-Sedge.—The characteristic features of the profile in the Alpine Dryas-Sedge stand (fig. 2) were: 1) the peat layer containing numerous rocks, between 0 and 5.25 inches; 2) the change from clay loam with rocks to silt with rocks and sand to mostly gravel and rocks at 15.5 inches; 3) excellent drainage to 35 inches where seepage appeared; 4) the deep penetration of the roots, with the working depth at 20.5 inches and the maximum depth at about 35 inches, most of the larger roots above 10.5 inches; pH 4.6 in the lower horizons to 5.8 in the surface horizon.

Detailed description of the soil profile:

0–0.75 inch—dark gray brown (4/2–10YR), well decomposed organic matter with very little fine silt or clay intermixed, plant crowns and roots numerous, pH 5.8.

0.75–5.25 inches—dark reddish brown (3/3–5YR), peat or muck, very well decomposed, very light in weight, rubs into a paste which is only slightly sticky, contains very little mineral matter, can be dug out in blocks of turf 3 to 5 inches thick and in places between rocks extends down to 7 inches, sharply edged usually flat rocks up to 4 × 8 inches are common and increase with depth, rocks rarely protrude above surface, roots very numerous, pH 5.4.

5.25–9.50 inches—variable, dark brown (3/2–7.5YR) to dark gray and gray (4/1 to 5/1–10YR), clay loam with much organic matter in it, picks out with an ice-pick in irregular blocky structures which break into smaller and smaller aggregates, rocks and gravel abundant, roots very numerous, pH 5.4.

9.50–15.5 inches—olive gray (5.2–5Y) silt with much gravel and fine sand; more compact especially in the upper part than the horizon above or the one below; picks out in irregular blocky structures which break crisply into smaller aggregates, gravel particles and single grains; occasional rocks; roots abundant in upper inch but become infrequent immediately below; pH 5.0.

15.5–24.0 inches—variable in color from olive gray (5/2–5Y) to pale olive (6/3–5Y) to dark gray (4/1–10YR); silt with many sand particles in it between the coarse gravel and rocks; horizon consists mostly of coarse gravel with slight structural development; roots infrequent; pH 4.6.

24.0–36.5 inches—prevailing color is olive gray (5/2–5Y), mostly gravel and rocks with sand and a small amount of silt between the rocks, this horizon is wetter than the one above and becomes increasingly moist to depth of about 35 inches where seepage flow is pronounced, roots infrequent to scarce occurring mostly on flat surfaces of rocks where a little silt has accumulated and extend between the rocks to about 35 inches, pH 4.6.

Relation to solifluction.—In the Alpine Dryas-Sedge stand, where no indications of solifluction were evident, the surface and internal drainage was good, and water from higher land did not overflow it. The presence of species such as *Carex bigelowii,* and *C. membranacea,* which are characteristic of the solifluction stand, may indicate that if additional water became available, this stand might readily develop into an Alpine Sedge stand and undergo solifluction. The presence of these species and other sedges may be the beginning of the Alpine Sedge type and of a solifluction area because the accumulating peat tends to increase the water content.

The solifluction areas here usually occur in the form of terraces with the upper parts gently to steeply sloping and with the lower ends as steep scarps. Slippage apparently occurs at the bottom of the peat layer and may also occur at the surface of the frozen layer. The compact silt layer at a depth of about 7.5 to 10 inches in the Alpine Sedge stand is highly impervious to water, it is slippery, and the peat layer above separates from it very readily, forming widespread cleavage planes. Water stands on the surface in many spots and in a few places it flows down the gradual slope. Portions, or large areas, of this stand apparently slide downslope when the forces of the weight of the water-soaked peat, the seepage of water especially at the lower surface edge of the peat, the slippery upper surface of the silt layer, and the good traction afforded by the frozen layer exceed the resistance of the terrain such as rocks and of vegetation. Near the lower end of this stand, where the slope is steeper, running water had formed channels above some of the hummocks, facilitating the downslope movement by detaching them from the mass above. The weight of snow and frost action probably also play a part in the downslope movement of these hummocks.

Description of a solifluction terrace.—A pronounced terrace or "wave" (fig. 3) was examined near the stands described above. It was characteristic of many other terraces in this vicinity, located on an east-facing slope of 5° to 10°. The vegetation on it was very similar to that of the Alpine Sedge stand, and the indications were that it was moving downslope over vegetation and soil similar to the Alpine Dryas-Sedge stand described previously. The lower edge or scarp of the terrace was 3 to 5 feet high and it was irregular because some parts were advancing more rapidly than other parts. It appeared that due to pressure from upslope the turf in many places had separated along horizontal cracks on the steep slope of the scarp. Some of these pieces of turf had continued to grow at the base, covering up the Dryas-Sedge community, and some had become covered up by the advancing margin of the turf and peat layers, below which could be seen the soil of the Dryas-Sedge vege-

FIG. 3. Solifluction terraces near Eagle Summit. Alpine Sedge vegetation on the terraces, Alpine Dryas-Sedge type on the slope below the terraces. East-facing slope of 5 to 10°. August 7, 1949.

tation. About 8 or 10 inches upslope from the edge, below a layer of peat and lying upon the former surface of the Alpine Dryas-Sedge type, was a horizon of silt with intermixed gravel, sand and rocks very similar to the horizons below 0.75 inch in the soil profile of the stand of the same type described above.

The area above the scarp was saturated with water at the surface and many small pools of water were encountered as close as 10 feet of the upper margin of the scarp. Examination of a profile about 20 feet upslope from the margin showed close similarities to the profile in the Alpine Sedge stand already described. The peat layer was about 7.5 inches thick, the silt-gravel horizon was slightly thicker, being about 21.5 inches thick, the former surface was encountered at 29 inches, and frozen ground at 30 inches. Water seepage was active just below the peat layer. The silt-gravel horizon was very compact, much more so than the gravelly rocky layer of the former surface horizon, and highly impervious to water. All of the layers were wet, but the silt-gravel layer prevented much of the water from penetrating below the peat. The peat, therefore, served as a collection reservoir for water. It is significant that none of the water flowed out of the lower end of the terrace onto the much drier Dryas-Sedge stand below.

It appeared clear that the entire mass of the terrace—vegetation, peat, and silt-gravel horizon—has been moving downslope mostly on the former surface, and probably in places on the surface of the frozen ground or at the seepage layer at

the bottom of the peat. The weight of the water-logged peat and the numerous rocks and gravel particles, the seeping water, and the flow capacity of the silt forces the mass down the slope.

Taber ('43), who had studied solifluction terraces or "benches" intensively on Eagle Summit, as well as on 12-Mile Summit on this highway and on mountains north of Nome, stated that the scarps are extremely steep, even overhanging slightly in front, that the detritus consists of fine silt with numerous angular fragments of the highly schistose country rock, that the vegetal covering is thickest on the face of the scarps and thinnest on top and near the rear where occasionally absent, and that on top of several of the terraces the turf had been crumpled into wrinkles near the frontal scarp. "The benches examined do not flow as a viscous mass, nor do they slide forward on their bases. The turf on the face of the frontal scarps is not stretched thin or ruptured, although it offers very little resistance to tension. Nor is the turf thickened or crumpled by thrust in front of the scarp. The detritus remains frozen throughout the summer except for a very thin layer on top" (to within 12–15 inches of the surface on Aug. 26, '35, on west slope of Mount Bryntsen, near Nome). "The scarp gains in height through additions of turf which slips forward on the thawed layer. . . . According to this hypothesis the benches grow and advance chiefly through freezing and thawing, the slow accumulation of detritus back of the vegetal mats, and the incorporation of plant remains in the soil. After the mat protecting the face of the scarp becomes so thick that the thawing during the short summers cannot penetrate, the downward advance of the bench becomes extremely slow. The lobate form of the benches, resembling mud- and lava-flows, gives an erroneous conception of their rate of growth and downward movement."

The present author agrees with Taber in the main, but has observed ruptured turf on the face of the scarp, apparently due to pressure from upslope. The author also gives greater importance to the influence of the seepage water, the flow capacity of the silt layer, and the weight of the water-saturated peat in causing sufficient pressure to force the mass downslope.

Frödin ('18) distinguished 3 kinds of terraces in Swedish Lappland: 1) Stripe-like terraces, lower than the glacier-like flows, a meter or so wide, about 1.5 meters long, and 1 dm high at the lower end. The vegetation, consisting of sedges, heath plants, mosses, lichens and few forbs, offers much resistance to earth flow, especially when the upper soil layers are not thick and the roots of phanerogams are frozen in the permafrost (*"tjälë"*). Stronger plants may invade and fix the lower part of the flow, or moister conditions may produce a more active flow. 2) Flowing terraces, several meters wide, distal end about 2 dm high and perpendicular, with dense firm vegetation, of sedges, grasses, mosses, lichens, etc. 3) Stabilized terraces, distal end with 45° or less slope and because of the accumulation of peat in the lower part of the terrace and the character of the vegetation stabilization had existed for a long time. Frödin states further that in the Alpine zone the distal ends of terraces may be meters high. The largest terraces have the best developed vegetation, he states. Tongue-like structures may form which are pushed slowly downslope. Under the plant cover a sliding ("Untergleidung") may occur, which gradually pushes the distal end downslope. In time the vegetation and the increasing height of the terrace may be able to counteract the downward pressure of the upslope mass. When snow-melting occurs suddenly and simultaneously with heavy rainfall, the earth mass under the plant cover may become a viscous silt mass which can break through because of its pressure. If the slope is steep enough this mass pushes onto the plant cover below and may tear it loose and cause an earth slide. On more gentle slopes half-

moon-shaped turf-mounds may occur, separated by patches of silt, upon which the turf-mounds slide. Lower down on more gentle slopes the mounds may have been pushed close together, and the vegetation has formed a closed cover.

Frödin pointed out the influence of abundant water, the flow capacity of the silt layer, and the pressure exerted by the land mass. He emphasized the retarding action of vegetation on the earth flow and its influence in building up the height of the terraces. In contrast to his statement that peat indicates a stabilized terrace, which may be the case in the region that he studied, this does not appear true on Eagle Summit where the accumulation of water by the peat tends to aid movement, at least not to retard it.

Mount McKinley Park (Station M)

Sable Pass.—Solifluction terraces are common on north-facing slopes in the vicinity of Sable Pass, at an elevation of about 3,900 feet, in Mount McKinley National Park. On August 21, 1949, the vegetation on one of these terraces was analyzed by the point-contact method, and the soil profile described (fig. 4). The detailed analysis is given under "Alpine Sedge Mt. McK." in table II. *Carex bigelowii* far exceeded any other species in the cover and in the frequency of occurrence. In contrast to the similar stand on Eagle Summit, no *Eriophorum* was found here, and other species of *Carex* occurred infrequently. *Salix polaris,* not found on Eagle Summit, was next in abundance at Sable Pass, and *Equisetum arvense* rated third. Mosses were much fewer in the Sable Pass stand than on Eagle Summit. The striking resemblance in the appearance of the two stands was due to the abundance of *Carex bigelowii* in both; the chief difference was in the much larger number of species and individuals in the Sable Pass stand, with 41 species and 1,110 hits compared to 19 species and 1,029 hits at Eagle Summit.

The wave-like terrace studied in detail was on the lower part of a north-facing slope of 10 to 15°. *Carex bigelowii* reached a height of 8 to 12 inches. On the soil surface was a layer about an inch thick of partly decomposed vegetation, and above this a loose layer, 2 to 4 inches thick, of dead leaves and stems, chiefly *Carex,* and moss.

FIG. 4. *Carex bigelowii* sod and profile in solifluction terrace at Sable Pass, Mt. McKinley National Park. Three former surface horizons and frozen ground at 46 inches were found in this profile. Elevation about 3,900 feet. North-facing slope of 10 to 15°. Ruler is one foot long. August 21, 1949.

Characteristic features of the soil profile (fig. 4) were: 1) the very dense and tough sod and the dense mass of roots of *Carex* chiefly; 2) the large number of roots to the deep working depth of 38 inches and the great depth of the maximum penetration of the roots, 46 inches; 3) the scarcity of peat; 4) the presence of 3 former surface horizons, due apparently to solifluction "waves"; and 5) frozen ground at 46 inches.

Detailed description of the soil profile:

0–1.5 inches—dark reddish brown (3/3–5YR), mostly organic material, fibrous, with

moderate amount of silt and occasional angular gravel fragments and sand particles; picks out in very loose irregular pieces which break down into fine aggregates, roots very numerous, moist, pH 6.0.

1.5–12.5 inches—mottled, strong brown (5/6–7.5YR), silt with much fine silt or clay and some sand, to gray brown (5/2–10YR), similar to the strong brown parts but containing less fine silt; many rocks and much gravel throughout; picks out with an ice-pick in irregularly sharply angled structures which break into smaller aggregates; feels rather crisp; roots very numerous; pH 4.6.

12.5–22.0 inches—dark reddish gray (4/2–5YR), silt loam with occasional gravel and sand particles, fewer rocks than in the layer above, somewhat peaty in spots; picks out in fairly soft irregular structures up to ½ inch long which break down into smaller aggregates; remains of old roots were found; live roots, especially fine ones, very numerous; pH 5.0; apparently a former surface horizon.

22.0–26.0 inches—yellowish brown (5/6–10YR), sand and gravel with moderate amount of silt; roots very numerous and coarser than in the layer above; pH 5.4.

26.0–33.5 inches—closely similar to the 12.5–22.0-inch layer, apparently a former surface horizon, roots (especially fine ones) very numerous, pH 5.4.

33.5–37.0 inches—closely similar to the 22–26-inch horizon, fine roots numerous.

37.0–40.5 inches—dark gray brown (4/2–

TABLE II. *Point-contact analyses of Alpine Sedge stand and Sedge-Heath-Sphagnum bogs in Mt. McKinley Park and near Healy*

Species	Alpine Sedge		Sedge-Heath-Sphagnum bogs			
	Mt. McKin.		Mt. McKin.		Healy.	
	Total hits	Freq., per cent	Total hits	Freq., per cent	Total hits	Freq., per cent
Carex bigelowii	605	83.0	277	49.0	333	61.5
Carex spectabilis Dewey	27	5.0				
Carex bipartita All.	1	0.5				
Carex rotundata Wahl.			5	2.0		
Eriophorum vaginatum			546	48.5		
Luzula multiflora	11	5.5				
Sphagnum spp.			88	44.0	200	100.0
Equisetum arvense L.	103	19.5				
Equisetum variegatum Schleich.	11	4.0				
Calamagrostis canadensis ssp. *langsdorfii* (Link.) Trin.					61	18.0
Arctagrostis latifolia (R. Br.) Griseb.	7	1.5				
Poa arctica R. Br.					2	0.5
Poa sp.	8	2.5				
Trisetum spicatum (L.) Richt.	3	1.5				
Deschampsia ?	2	0.5				
Salix polaris Wahlenb.	132	35.5				
Salix reticulata	36	13.5	3	1.0		
Salix pulchra			x		46	9.0
Betula nana exilis			25	8.0	290	54.0
Ledum decumbens			105	19.0	297	46.0
Vaccinium uliginosum			63	16.0	140	29.5
Vaccinium vitis-idea			59	11.5	74	17.0
Vaccinium Oxycoccus L.			33	11.0		
Rubus chamaemorus			8	2.5	3	1.0
Andromeda polifolia L.			56	19.0		
Polygonum bistorta plumosum	15	7.0	1	0.5		
Polygonum viviparum	12	6.0			1	0.5
Cassiope tetragona (L.) D. Don.	7	1.5				
Dryas octopetala	38	8.5				
Anemone parviflora Michx.	15	7.0				
Dodecatheon frigidum C. and S.	2	1.0				
Pedicularis capitata	3	1.5				
Pedicularis labrodorica Wirsing			1	0.5		
Petasites frigidus (L.) Fries	12	4.5			2	0.5
Myosotis alpestris F. W. Schmidt	5	1.0				
Cardamine purpurea	9	3.0				
Stellaria laeta Rich.	5	2.5				

TABLE II.—*Continued*

Species	Alpine Sedge		Sedge-Heath-Sphagnum bogs			
	Mt. McKin.		Mt. McKin.		Healy	
	Total hits	Freq., per cent	Total hits	Freq., per cent	Total hits	Freq., per cent
Claytonia sarmentosa C. A. Mey.	5	2.0				
Ranunculus sulphureus Phipps.	2	0.5				
Artemisia arctica Less.	8	3.0				
Valeriana capitata Pall.	7	3.0				
Polemonium acutiflorum Willd.	4	2.0				
Aconitum delphinifolium DC.	3	1.5				
Anemone richardsonii Hook.	2	1.0				
Boykinia richardsonii (Hook.) Gray	2	1.0				
Empetrum nigrum			63	16.0		
Arctostaphylos alpina			3	1.0		
Tofieldia pusilla			5	1.0		
Epilobium angustifolium L.					2	0.5
Seedling	1	0.5				
Cladonia rangiferina (L.) Web.			41	20.5		
Cladonia sylvatica (L.) Hoffm.			1	0.5		
Cetraria cucullata (Bell.) Ach.			33	16.5		
Cetraria islandica (L.) Acb.			7	3.5		
Thamnolia vermicularis (Sw.) Schaer.			1	0.5		
Pleurozium Schreberi (Willd.) Mitt.			25	12.5		
Hylocomium splendens (Dedw.) Bry. Eur.			11	5.5		
Dicranum sp.			6	3.0		
Aulocomnium palustre (Web. and Mohr) Schwareg.			7	3.5		
Polytrichum sp.			1	0.5		
No hits	5	2.5			+	
Total number of hits	1110		1474		1451	
Additional species in stands but not hit						
Claytonia sp.	x					
Sedum roseum (L.) Scop	x					
Moss	x					
Saxifraga lyallii Engler	x					
Saussurea angustifolia	x					
Saxifraga hieracifolia Wallst. and Kit.	x					
Lichens	x					
Papaver sp.	x					
Equisetum sylvaticum L.					x	
Senecio frigidus Less.			x			
Carex tenuiflora Wahl.			x			
Lycopodium annotinum L.			x			

2.5Y), silt with occasional gravel pebbles and coarse sand, roots infrequent.

40.5–46.0 inches—yellowish brown (5/4–10YR), sandy silt with much clay or fine silt (can be rolled into fine wire) and with scattered gravel, becoming much more gravelly at 44 inches, roots infrequent.

46.0 inches—frozen.

The chief evidences of solifluction on this slope were the general appearance caused by the wave-like terraces with a melting snowdrift near the summit of the slope as late as August 21, and the presence of 3 former surface horizons in the soil profile. Movement appears to have been slower than at Eagle Summit, probably because of the drier conditions in the former location, the much smaller amount of peat, the more abundant and much deeper penetration of the roots, and the greater depth to the frozen ground, 46 inches as compared to 24 inches. A horizontal cleavage plane, as found between the peat and the silt-gravel layer at Eagle Summit, was not found at Sable Pass.

The south-facing slope, across the valley from the stand described above, did not show the occurrence of solifluction.

The vegetation varied considerably and was largely of a grass-heath type. Usually the stand was open, with scattered tufts and lichens and mosses between them. The lichens and mosses formed a complete cover where the tufts were close together, but much bare, gravelly surface was exposed when the tufts were more scattered. The species contributing most to the cover and of highest frequency, in addition to the lichens and mosses, were *Festuca altaica* with leaves 10 to 12 inches tall, *Vaccinium vitis-idea, V. uliginosum* with branches 4 to 5 inches tall, *Betula nana exilis* about 10 inches tall, *Empetrum nigrum, Dryas octopetala,* and *Carex spectabilis.* Not including the lichens and mosses a total of 41 species and 919 hits were recorded in a stand where the tufts were not widely scattered. The characteristic features of the soil profile were: 1) The closeness (2.25 inches) of the gravel to the surface; 2) The dark gray brown layer at 1.25–2.25 inches, appearing leached; 3) Brown coloration to a depth of 35 inches; 4) The good distribution and large number of roots, mostly of *Festuca altaica,* to the working-depth of 24 inches; and 5) The maximum-depth of the roots at 32 inches which is fairly shallow.

Wonder Lake.—(1) Sedge-Heath-Sphagnum Bog. This bog was situated on a south-facing slope of less than 5° on the north side of Wonder Lake, in Mount McKinley National Park, at an elevation of about 2,000 feet. This stand was surrounded by a heath-sedge type which was darker green than this one. Scattered throughout the stand were tussocks about 6.5 inches high, formed chiefly by the growth of *Eriophorum vaginatum,* with leaves 6 to 12 inches in height. Green moss, especially *Pleurozium schreberi* and *Hylocomium splendens,* and living *Sphagnum* extended about 3 inches above the dead *Sphagnum* and moss on the hummocks. Lichens formed a loose layer on top of and between the moss plants and between the *Eriophorum* stems. Lichens also were found on the sides of hummocks and a few on the dead sedge tufts. As shown in table II *Eriophorum* provided most of the cover in this stand, but *Carex bigelowii,* with about one-half as much cover, was similar in frequency. Other important species, in addition to *Sphagnum* spp. and lichens, were *Ledum decumbens, Vaccinium uliginosum, V. vitis-idea, V. oxycoccus, Empetrum nigrum, Andromeda polifolia,* and *Betula nana exilis.* Detailed studies were made of this stand and the surrounding vegetation on August 24–25, 1949.

Characteristic features of the soil profile were: 1) The surface layer of light brown, slightly decomposed sphagnum which was about 10 inches thick in the depressions and up to 2.5 inches in the hummocks; 2) Decomposed peat at 2.5–6.5 inches in the hummocks, lacking in the depressions; 3) Peat extended below the surface of the depressions to the frozen ground at 20 inches and below the surface of the hummocks to frozen ground at 26.5 inches.

Detailed description of the soil profiles:

a. Depression

0–2.0 inches—slightly decomposed plant remains, mostly sphagnum, roots not numerous.

2.0–10.0 inches—light brown sphagnum, decomposed very little in the upper third of this horizon, the lower part partly decomposed and brown in color, transitional to the horizon below, roots very numerous.

10.0–20.0 inches—well decomposed peat with very small amount of silt, water oozes out of this layer readily carrying some peat with it, frozen ground at 20 inches, roots numerous to about 17.5 inches which was the working depth, maximum depth 20.0 inches.

b. Hummock

0–2.5 inches—mostly light brown dead sphagnum which is only slightly decomposed, roots numerous.

2.5–6.5 inches—very dark brown peat, well decomposed, small amount of silt, roots very numerous.

6.5–16.5 inches—fibrous, brown peat, lower part transitional to the layer below, roots very numerous.

16.5–26.5 inches—closely similar to the 10–20-inch horizon above, frozen ground at 26.5 inches, working depth of roots at 24 inches, maximum depth 26.5 inches.

FIG. 5. Sedge-Heath community at Wonder Lake, Mt. McKinley National Park, characterized by hummocks and flat depressions with clay or fine silt surfaces. Elevation about 2,000 feet. South-facing slope of less than 5°. Chief species: *Carex bigelowii, Vaccinium uliginosum, V. vitis-idea, Betula nana exilis,* and *Empetrum nigrum.* August 25, 1949.

This stand was surrounded by a more hummocky type, described below, in which definite evidence was found of solifluction. Both of these types were saturated with water and seepage was taking place from a pond at a slightly higher elevation into this area. It appeared probable that solifluction was occurring in this area as a whole, and unquestionably in parts.

(2) Heath-Sedge Community. The stand described immediately above was surrounded by a much larger area of a Heath-Sedge type of vegetation (fig. 5), and was studied on August 24–25, 1949. It consisted of small ridges and hummocks, about 1 to 3 feet high and a foot to 6 or 8 feet wide, separated by narrow furrow-like depressions or more or less circular, basin-like areas up to 10 or 12 feet in diameter, often arranged in a roughly step-like series. The ridges and hummocks were soft and cushiony because of the mass of herbage on them, but the depressions were rather bare with usually a wet surface of fine silt with scattered gravel pebbles.

The more common species growing on the ridges and hummocks were *Vaccinium uliginosum* (ab.),[3] *Betula nana exilis* (ab.), *Ledum decumbens* (ab.), *V. vitis-idea* (ab.), *Empetrum nigrum* (ab.), *Carex bigelowii* (ab.), *Arctagrostis latifolia* (freq.), *Salix pulchra* (inf.), *Polygonum bistorta plumosum* (inf.), *Poly-*

[3] Meaning of abbreviations: ab = abundant, plants numerous with uniform distribution; v.ab. = very abundant; freq. = frequent, plants not numerous, distribution fairly uniform; inf. = infrequent, plants not numerous, scattered, distribution usually irregular; sc. = scarce, plants few and scattered.

trichum sp. (ab.), *Pleurozium schreberi* (Willd.) Mitt. (freq.), *Aulocomnium palustre* (freq.), and many kinds of lichens, which were more abundant on the drier hummocks along with *Loiseleuria procumbens* (L.) Desv. The most common species in the depressions were *Carex capillaris* (freq.), *Juncus castaneus* J. E. Smith (freq. to ab. and typical here), *Juncus albescens* (Lge.) Fern. (freq. to ab. and also typical here), *Arctagrostis latifolia* (freq.), *Salix pulchra* (inf.), *Sphagnum* spp. (inf., invading), *Tofieldia pusilla* (sc.), *Lycopodium selago* L. (inf.), *Carex bigelowii* (beginning to form tussocks in some of the depressions), a hepatic which formed the main cover in some, *Polytrichum* sp. (invading in spots), and a few lichens such as *Cladonia amaurocraea* (Floerke) Schaer. and *Stereocaulon* sp. which were inf.; various species of heath plants, especially *Vaccinium uliginosum*, were invading the margins of many of the depressions. The chief species occurring in the shallow water in some of the depressions were *Juncus castaneus* (freq. to ab.), *Hypnum molluscum* L. (v. ab.), *Drepanocladus* sp. (v. ab.), and a hepatic (freq.).

Detailed descriptions of soil profiles:

1. The soil profile was examined in a trench dug into the north side of a rather flat-topped ridge (fig. 5) which was about 6 feet wide and 1.5 to 2 feet higher than the 10-foot depression which adjoined it on the north. The surface of the depression was flat and was composed of fine gray silt, or clay, with scattered gravel. It was mostly bare of vegetation. It appeared that the ridge was being pushed out of the depression, downslope. On the surface of the ridge was a soft, dense layer, about 4 inches thick, consisting of mosses, lichens, dead leaves and stems, and the interwoven stems and leaves of living plants. Under this was a layer of partly decomposed leaves, etc., about 1 inch thick.

0–4 inches—dark reddish brown fibrous peat, somewhat decomposed, little silt.

4–21 inches—light yellowish brown (6/4–10YR) to gray (5/0–2.5YR) fine silt with moderate amount of gravel, the lowest 3 to 4 inches with much gravel and sand; the clay was massive, wet in the upper part and moist in the lower part, one's feet sink into it rapidly and when tapped on the side of the trench several square inches are affected as if it were a firm jelly. This horizon is similar to the surface of the depressions where several square feet can be shaken by tramping on it. These characteristics indicate flow capacity, especially on slopes and where there is room for a mound or ridge to move into. The silt layer shows considerable imperviousness to water.

21–24 inches—dark brown, fairly well decomposed peat, moderately moist, a few fibers evident, with small amount of gravel. This appears to be a former surface which had been covered by a hummock pushed over on it.

24–43 inches—sandy and gravelly with much silt and apparently some clay, very wet, olive gray (5/2–5Y), 4- to 6-inch rounded cobbles throughout, roots seen to depth of 40 inches, no frozen soil encountered due possibly to water standing in the depression above for a long time and absorbing and transmitting much heat.

2. A profile was examined about 30 inches from the above, on the opposite side of the ridge, and downslope from it. Mosses, lichens, stems and leaves of *Ledum, Betula, Carex,* etc., formed a dense layer 4 to 5 inches thick on the surface and below this was a 2-inch layer of plant debris. The lower part of this ridge was quite messed up by the irregular distribution of stems and leaves, giving the appearance of being pushed downslope. The ridge on this lower slope was subdivided into small hummocks with cracks between them, which became evident when the dense cover was opened. At the lower periphery of the ridge many plants were growing mostly in a horizontal direction, evidently due to pressure from upslope.

0–11 inches—loose and very fibrous peat, dark reddish brown, without any silt, more decomposed in the lower part, roots very numerous.

11–22 inches—dark reddish brown (3/2–5YR) silt loam with much organic material, gravel and stones become more numerous with depth, cobbles infrequent up to 4 to 6 inches long; transition from the peat horizon above is very pronounced, giving the appearance that the peat layer, especially the upper 7 inches of it, had been pushed over onto this silt-loam horizon.

22–29 inches—silt loam, reddish brown (4/3–5YR) turning to gray brown (5/2–2.5Y) in the lower part, moderate amount of gravel and sand with much organic material, gravel and sand increase in quantity with depth, 4- to 6-inch cobbles scattered throughout. The lowest 3 to 4 inches of this horizon are saturated with water, which does not penetrate into the layer below.

29–43 inches—similar to the 4–21-inch horizon in the upper side of this ridge, fine silt with moderate amount of gravel in the upper part, highly impervious to water, roots seen penetrating into this layer, no frozen ground to 43 inches.

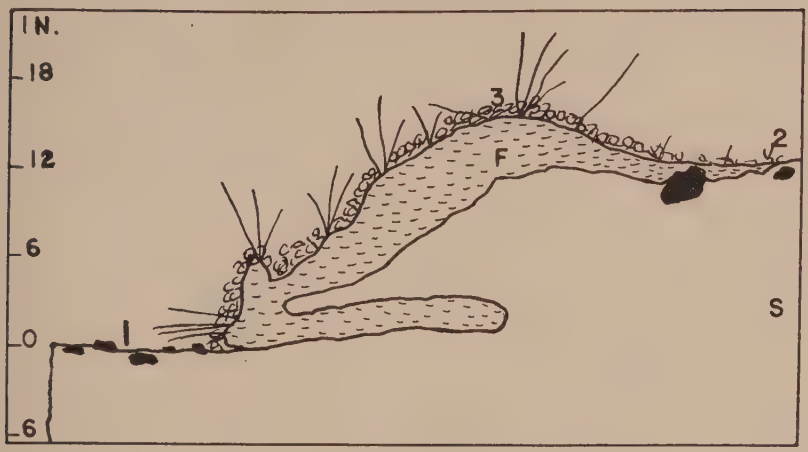

FIG. 6. Profile of a hummock which has moved about one foot from the higher depression at the right into the lower depression at the left. 1 = lower depression, 2 = higher depression, 3 = hummock, F = fibrous organic material partly decayed and covered with living vegetation, S = fine silt, solid shading represents stones. Note surface organic material under the clay to left of center, and the fine silt extending from the surface of the lower depression to the surface of the upper depression. General slope is southerly of less than 5°. Sedge-Heath community, Wonder Lake, Mt. McKinley National Park. August 5, 1949.

When the trenches were dug into the fine silt layer water oozed rapidly and in places flowed like a spring from the 3- to 4-inch gravelly portion of the 22–29-inch layer. The wet slippery surface of the 29–43-inch layer provided excellent traction for the mass above. It appeared probable that water from the depression above may seep into the gravelly portion just above the 29–43-inch horizon, because the latter appears to be continuous with the material composing the surface layer of the depression. The movement of water which presumably occurs just above the 29–43-inch layer would be an important factor in the movement of the ridge.

Detailed examination of the profile (fig. 6) of another small hummock on the uphill side of the depression, described above, showed, by the vegetation that had been covered up, that movement of at least a foot had taken place onto the depression. Other mounds and hummocks bordering this depression, and elsewhere in the stand, also showed encroachment into the depressions (fig. 5). The hummocks and ridges were usually bordered on the upslope side by similar depressions, and the fine silt layer of one depression often sloped upward, as if pushed, to become the surface of a higher depression. Apparently solifluction of ridges and hummocks was occurring throughout this stand. The depressions were evidently being occupied on their upper portions and being made bare on the lower parts. The causes of the solifluction seem to be found in the nature of the material in the fine silt layer, the abundance of water at least in certain periods of the year, seepage of the water, and the effects of freezing and thawing.

Taber ('43) stated that the differential uplift of the soil surface is caused by local differences in the segregation of ice due to differences in soil texture or to differences in soil cover. Water segregates during the freezing of fine-grained soils to build up layers of pure ice. "Where the surface is insulated by a thick mat of vegetation and peat, except

for small bare areas, freezing begins first on the exposed areas, and water may be drawn toward them to cause greater heaving at these places. . . . Low mounds or frost boils often develop as a result of slightly greater heaving at points most favorably located for early freezing and the formation of segregated ice."

Much in Frödin's paper ('18) on mounds (*"Lehmhügel, Lehmbeulen"*) is pertinent here. He wrote that round, bare spots, scattered in dense vegetation at lowest elevations in mountains and usually in moors and heaths (in Swedish Lappland), with diameters from 0.5 to 5.0 meters, may be so numerous as to give a characteristic appearance to the area. They may rise 0.5 to 2 dm above the plant cover and consist mainly of *"Gärlehm"* with intermingled smaller and larger stones. The Gärlehm may pass through the peat layer and be connected with the silt or clay layer upon which the peat lies. It clearly arose from the fine silt layer by a vertical movement passing through the peat horizon. Often the edges of the peat layer adjoining the mound have been turned upward by the upward penetrating fine silt mass. Frödin's paper contains some excellent illustrations of this kind of mound formation.

West of Healy (Station H)

Sedge-Heath-Sphagnum Bog.—Solifluction appeared to be occurring on the lower part of a north-facing hillside with a slope of about 5°, about 5.5 miles west of Healy, located on the Alaska Railroad north of McKinley Park. The stand, studied on August 19, 1949, was on a mostly gentle slope, at an elevation of about 2,600 feet. The surface was hummocky, due to the growth of *Sphagnum,* which was 7 to 8 inches thick in the depressions and 11 to 12 inches additional in the hummocks. The most important plants (see table II), in addition to *Sphagnum* spp., were *Carex bigelowii* with leaves extending about 8 inches above the tops of the hummocks and 12 to 16 inches above the depressions, *Ledum decumbens* with stems 4 to 12 inches long, *Betula nana exilis* growing mostly in the depressions with stems 10 to 18 inches tall, and *Vaccinium uliginosum* which was mostly on low hummocks with stems 4 to 8 inches long and with the roots mostly in the lower part of the *Sphagnum* layer. *Carex bigelowii* plants had died in places, probably due to the effect of the *Sphagnum,* but generally it was sending out new roots at higher levels as the *Sphagnum* increased in height. The original crowns of *Carex* were found at the bottom of the *Sphagnum* layer. Other less important species in this stand were *Vaccinium vitis-idea, Calamagrostis canadensis* ssp. *langsdorfii, Salix pulchra,* and several minor ones. The total number of species found in this bog was 14, and the total number of hits 1,451.

Detailed description of the soil profile:

0–5 inches—horizon below the sphagnum layer, dark reddish brown (2/2–5YR), fibrous peat with many coarse stems in it as well as much fine material, containing a very small amount of silt, saturated with water, roots very numerous, pH 4.4.

5–10 inches—gray brown (5/2–10YR), fine silt, slightly sticky, containing scattered grains of fine sand, in center of this horizon was a 1-inch layer of dark brown (4/2–7.5YR) peat which was fairly well decomposed and contained a moderate amount of silt, roots numerous to the frozen ground at 10 inches, pH 4.8.

The appearance of some of the hummocks and of the spaces between some of them indicated that local movement had occurred. The general appearance of the entire stand, the water-saturated soil, the shallowness of the frozen ground, and the topographic features including steeper land upslope from which drainage is received provided favorable conditions for solifluction.

Near Kotzebue (Station K)

Hummocky Sedge-Heath.—The tundra adjacent to the village of Kotzebue varies considerably, with brackish sedge-marsh adjoining the inlets and ponds which are subject to overflow during storms, the wind and waves forcing the water inland,

to Sedge-Heath hummocky communities, fresh-water sedge marshes, and long, fairly wide gravally former beaches, all above the storm waters. These stands were studied on August 10, 1949.

The Sedge-Heath hummocks occur on land that is fairly level to gently rolling. Ridges and hummocks, from 2 to about 15 inches high, more or less surround the depressions, which vary from less than a foot to several feet in diameter. Often the ridges may be in the form of long irregular lines, and low hummocks may be scattered in the depressions. The hummocks and ridges vary from about 0.5 to 3 feet wide and are rather flat-topped. The vegetation in the depressions consisted mostly of sedges such as *Carex rariflora* (Wahl.) J. E. Smith, *C. aquatilis* Wahl., *C. glareosa* Wahl., *C. subspathacea* Wormskj., *C. rotundata, Eriophorum angustifolium, E. chamissonis* C. A. Mey., and a few other species including the mosses *Drepanocladus exannulatus* (Bry. Eur.) Warnst., and *Calliergon* sp., *Petasites frigidus, Rumex arcticus* Trautv., and *Hippuris vulgaris* L., the last in shallow water. On the hummocks the chief species were *Empetrum nigrum* (com., ab.), *Ledum decumbens* (com., ab.), *Vaccinium vitis-idea* (com., ab.), *Rubus chamaemorus* (ab.), *Festuca rubra* L. (freq. to ab.), *Eriophorum vaginatum* (freq.), *Salix ovalifolia* Trautv. (freq.), *Betula nana exilis* (freq.), *Vaccinium uliginosum* (freq. to ab.), *Arctostaphylos alpina* (freq.), *Arctagrostis latifolia* (inf.), *Ranunculus lapponicus* (inf.), *Hierochloa pauciflora* R. Br. (sc.), *Sphagnum* spp., mosses, lichens including *Cetraria cucullata, C. islandica, Thamnolia vermiculatus, Cladonia rangiferina,* and *C. alpestris* (L.) Rabenh., as well as some relicts from the depression stage. On the uppermost, driest parts of the hummocks common species were *Pedicularis lanata* Cham. and Schlecht., *Hierochloa alpina, Poa alpina* L. probl., *Festuca rubra, Calamagrostis canadensis* ssp. *langsdorfii, Carex bigelowii,* and lichens including *Thamnolia vermicularis, Parmelia* sp., *Sphaerophorus globosus* (Huds.) Wainio., *S.* sp., *Cladonia uncialis* (L.) Web., and *Alectoria* sp. Some of the earliest invaders into the wet sedge marsh were species of *Sphagnum* such as *S. fuscum* (Schimp.) H. Klinggr. Somewhat later invaders were *S. tenellum* Pers., other spp. of *Sphagnum,* and *Carex rariflora.* Willows and birch may invade the sedge marsh as first pioneers, but more often follow *Sphagnum. Eriophorum vaginatum* tussocks usually develop in a late stage of the sedge marsh. These tussocks may grow to a height of 6 to 10 inches and a diameter of 6 to 12 inches, and may in places extend above the general height of the heath. *Arctagrostis latifolia* may also be one of the early invaders of the sedge marsh. Various species of moss (Hypnaceae) are more often first invaders than *Sphagnum* spp., and appear to build low mounds rather rapidly. Following the early invaders were heath plants and the grasses.

A trench was dug to examine the soil profiles under a typical hummock and an adjoining depression. The hummock extended about 6 inches above the surface of the depression.

Detailed descriptions of the soil profiles:

1. *Depression.* Vegetation chiefly sedges and moss, sedge leaves extended 4 to 6 inches above the 2-inch layer of dead leaves and stems, in which green moss (*Hypnaceae*) was fairly abundant.

0–1.25 inches—dark reddish brown (3/2–5YR), mostly decomposing organic matter (mucky), with small amount of fine silt in it, fibrous; picks out into soft irregular aggregates with roots intermixed; roots very abundant, rhizomes frequent; saturated with water.

1.25–2 inches—yellowish red (4/6–5YR), decayed organic matter with small amount of silt, on rubbing becomes very wet and smooth but only slightly sticky, fibrous; picks out with an ice-pick in soft lumpy aggregates with intermixed roots; roots very numerous.

2–4 inches—dark gray brown (4/2–10YR), wet silt containing much organic matter and many sand particles, fibrous; picks out in soft irregular aggregates with many intermixed roots; saturated with water; roots very numerous.

4–9 inches—very dark gray (3/1–10YR), partly decomposed organic matter with small amount of fine silt and many dead and very

many living roots; no small gritty particles as in the horizon above; picks out in soft blocky structures.

9–10.5 inches—dark reddish brown (3/4–5YR), peat, composed mostly of short pieces of plants, water-saturated, roots numerous, small stones infrequent in the lower portion.

10.5–12.25 inches—dark gray brown (4/2–10YR), peat with moderate amount of silt intermixed, picks out in soft aggregates, fine roots numerous.

12.25–14 inches—very dusky red (2/2–2.5YR), peat, mostly well decomposed with very small fragments of plants and moderate amount of silt, occasional small gravel particles, saturated, roots frequent.

14–15 inches—gravel with gray (5/1–10YR) clay in places and yellowish brown (5/4–10YR) sand in others, roots scarce.

The working depth of the roots was at 11.5 inches and the maximum depth at 15 inches. Frozen ground was encountered at 15 inches.

2. Hummock adjacent to above depression. The vegetation on this 6-inch high hummock consisted chiefly of *Empetrum nigrum, Salix ovalifolia, Festuca rubra,* and a few plants of *Carex* spp. The general height of the foliage reached 4 to 5 inches above the 2-inch layer of dead leaves and stems with scattered green moss. The depth to the frozen ground was 20 inches. The profile was irregular due to a peat wedge which extended from the frozen ground into the middle of the hummock and to within 6 inches of the surface. The surface horizon of the hummock, consisting of dark reddish brown, mostly decomposed organic matter, similar to the 0–1.25-inch layer in the depression-profile, varied in thickness from 5 inches on the east side to 3 inches on the west side and 2 to 3 inches on the top. The peat wedge was about 5 inches wide and consisted of mostly short, partly decomposed pieces of plants, similar to the 9–10.5-inch horizon in the depression-profile. The layers above the wedge had an upward to vertical position on the east and west sides of the hummock, and in the upper part of the hummock the layers were considerably mixed, except for the surface 2- or 3-inch horizontal layer. Below the wedge the gravelly fine silt or clay layer was also considerably distorted and in some places was more or less vertical. Apparently a thrust from below, probably arising from freezing or thawing, had forced the silt and peat up into the hummock. Examination of other mounds and ridges nearby failed to reveal similar structure. Usually the frozen ground extended upward a short distance into the hummock, probably because of the insulating influence of the vegetation on it.

3. Another hummock, about 10 inches high and about 2.5 feet in diameter, on a former gravelly beach, revealed two parts, the larger main portion and the smaller part on one side which appeared as having been split off. The vegetation on the beach proper consisted of a sparse cover of lichens and heath plants. A thin layer of about 1.5 inches of peat formed the surface horizon, under this a 1.5-inch layer of gray fine silt, which was underlaid by gravel. The silt layer continued horizontally under the hummock, except under the crack into which silt and some gravel extended upward for an inch or two. The top of this crack was about 4 inches wide and it became narrower toward the base, and it was occupied by a dense growth of heath, willow and birch plants, which also grew on the sides of the hummock. The top of the hummock was covered with heath and lichens.

A number of processes are undoubtedly involved in the formation of ridges and hummocks, and their disintegration. The various depths at which the frozen ground is found, in August, such as 10.5 inches in the heath-sedge type, 22 inches in the wet sedge type, and 27 inches in the barren, gravelly lichen-heath beaches, probably give rise when freezing occurs to various kinds of pressures. Soil materials vary from gravel to fine silt or clay and to peat. Some areas are well insulated by peat and vegetation, other areas poorly. Differences occur in the elevation and exposure of hummocks and depressions. The water-content varies from the lowest in the gravelly lichen-heath ridges and tops of some of the hummocks to water-saturated soil and standing water in the depressions and wet sedge type. Under conditions of freezing and thawing shifting of materials in the soil, as the upward thrusting of wedges of peat or silt, must occur frequently. Mounds and hummocks, whether started or enlarged by frost action or by vegetation growth, appear, in places at least, to go through a process of growth and disintegration. This may begin with the invasion of certain mosses and *Sphagnum* spp. in the sedge-marsh to form low mounds. Conditions are suitable on these low mounds for the invasion of other kinds of mosses and *Sphagnum,* followed by a variety of heath plants, willows, birch, and sedges adapted to drier ground, a few grasses,

and a variety of forbs. As the hummock enlarges, due to the accumulation of peat and litter, the vegetation becomes very dense. A few lichen species occur. In time the hummock may become so high that it is well exposed to the winds and the soil materials dry out more rapidly, and plants on the summit die. They are succeeded by species of lichens adapted to the drier, wind-exposed conditions, but in time they also die and more active erosion by the wind sets in. The protruding dead roots and stems of low shrubs continue, however, to give considerable resistance to the wind-driven rain, sleet, and snow.

The occurrence and formation of mounds and hummocks has been discussed by various writers (Troll '44, Muller '47, Taber '43, Frödin '18, Sharp '42, and others). Sharp ('42) stated that "most theories provide some mechanism whereby earth may be drawn up or forced into knobs chiefly by differential freeze and thaw. Fries suggests that an irregular or discontinuous cover of winter snow allows deeper freezing in some places than in others with consequent localized updoming which may be only partly destroyed by the succeeding summer thaw. Renewed freezing the following winter supposedly accentuates this upwarp. Many earth or peat hummocks have frozen cores, but others do not, and in the latter it seems that material has actually been forced into the mounds. Beskow suggests that the ground under the hummocks is less deeply frozen or does not freeze so quickly as the adjoining area owing to the better insulation provided by a thicker air-filled vegetative cover. The various soil structures along Wolf Creek [St. Elias Range, Yukon Territory] are attributed to vigorous frost action during the fall and spring, supplemented on slopes by solifluction. Intensity and frequency of freeze and thaw, constitution of surface debris, weathering and comminution, degree of slope, amount of water, drainage, height of water-table, vegetation, and depth to perennially frozen ground are all recognized as contributing factors which must be evaluated for each particular locality." It might be added that studies of permanently marked spots which can be plotted and in which measurements of the height and diameters of mounds can be made should be observed for a number of years, and at various times during the year, particularly at times of freezing and thawing.

A number of investigators have discussed the formation of mounds or hummocks by plant action and the succession of plants on them (Dachnowski-Stokes '41, Oswald '49, Polunin '48, Wenner '47, and others). Apparently it is a widespread occurence for mounds to grow so high that they become dry on the top and become covered with lichens; and with heath plants, sedges, etc., on the sides. Growth in height may follow winters of deep snow cover, drying of tops may occur in periods when snow cover is thin.

Sedge-tussock-Heath Tundra.—This stand, examined on August 12, 1949, was on the rolling tundra on the Baldwin Peninsula about a mile from the shore of Kotzebue Sound about 35 miles south of Kotzebue, almost on the Arctic Circle. The elevation was only 40 to 50 feet above sea-level, and the terrain was exposed to the strong westerly winds from Kotzebue Sound. The low gently rolling hills were covered chiefly by tussocks ("niggerheads"), 8 to 15 inches high, separated from one another by depressions, i.e., the general level from which the tussocks grew, by 0.5 to about 4 feet, averaging about 12 inches. The tussocks were about 8 to 24 inches in diameter, mostly about 12 inches. Walking was difficult because most of the tussocks do not support one's weight, and they form entirely too many obstacles when attempt is made to walk between them. According to report of the reindeer herder the amount of snow varies during the winter from a foot or more above the tops of the tussocks to below the tops of the tussocks, thus exposing them to the strong winter winds. Hard, compact drifts form in spots. This stand was typical of areas

grazed by reindeer for 1.5 to 2 months in the autumn.

The chief tussock formers are *Eriophorum vaginatum* and *Carex bigelowii,* both of which were abundant and dominant apparently. Other species were: *Betula nana exilis,* ab., chiefly in the depressions; *Ledum decumbens,* ab., chiefly in the depressions; *Arctagrostis latifolia* var., freq. in the depressions, inf. on steeper slopes of hills; *Empetrum nigrum* ab., depressions chiefly; *Vaccinium vitis-idea,* ab., depressions chiefly; *Sphagnum* spp., freq. to com. in depressions; *Rubus chamaemorus,* freq., depressions chiefly; *Arctostaphylos alpina,* inf., depressions chiefly; *Spiraea beauverdiana* Schneid., inf., slopes; *Salix glauca acutifolia* (Hook.) Schneider, inf., slopes; *Vaccinium uliginosum,* inf., depressions; *Petasites frigidus,* inf., depressions; and mosses and lichens in the depressions, on the sides and on the summits of the tussocks. The lichens are more numerous on the tussocks than in the depressions; especially *Cladonia alpestris, C. rangiferina* (up to 2 inches high), *Cetraria islandica, C. cucullata,* and *Alectoria nigricans* (Ach.) Nyl. A trench was dug through the extremely tough center of an *Eriophorum vaginatum* tussock and the general level on each side of it. The tussock consisted of a dense basal portion which extended 6 inches above the general ground surface, a dense tuft of dead and green leaves radiating outwards for several inches on all sides of this central core, and, at the summit, green leaves extended upward for 8 to 9 inches and the inflorescences to 12 and 15 inches. Branches of *Vaccinium vitis-idea* and *Betula nana exilis* extended into the foliage and over part of the tussock. Moss and heath plants formed a layer 3 inches thick on the general surface around the tussock. The substratum showed very little development. The surface horizon between 0 and 2 inches was brown clay. From 2 to 17 inches the dark gray clay was strongly mottled with strong brown. The roots were very abundant under the crown to a depth of 8 inches and elsewhere they were numerous to 16 inches. Between 16 and 17 inches the roots were only frequent. The working depth of the roots was at 16 inches and the ground was frozen at 17 inches. Evidence of solifluction was seen on some of the slopes.

Craigie Creek (Station C)

Alpine-sedge Marsh.—This stand, studied on July 26, 1949, was on a gentle slope at the base of steep mountain slopes in the Craigie Creek Valley at an elevation of about 3,100 feet in the Talkeetna Mountains. Water flowed into it from small streams which originated in the mountain slopes. It was poorly drained, although a few very small streams with gently flowing water occurred. It occupied about 5 acres. The surface was hummocky; the hummocks and ridges, usually at right angles to the direction of the slope, were 8 to 10 inches higher than the level depressions between them. The hummocks were soft and cushiony on account of the tangled mass of moss, roots, stems, and leaves on the surface. In many of the depressions water was standing, in others water oozed out rapidly from the substratum as one stepped on it.

The vegetation on the hummocks was generally 6 to 12 inches tall. The list of species and quantitative data on cover and frequency for the hummocks and for the depressions are given in table III. Species showing the greatest cover and frequency on the hummocks were *Eriophorum angustifolium, Carex pluriflora,* mosses, *Salix reticulata,* and *Sanguisorba sitchensis.* A total of 34 species, and 1,220 hits, were recorded. The vegetation in the depressions was sparser, only 673 hits were made and the total number of species was only 10. The chief species were the same as the first three listed above on the hummocks.

A trench was dug into one of the ridges and an adjoining depression, which was 9 inches lower, and had about 1 inch of water in it (fig. 7). A small dam was made at the edge of the depression so water

TABLE III. *Point-contact analyses of vegetation on hummocks and in depressions in Alpine Sedge Marsh stand, Craigie Creek, Talkeetna Mountains*

Species	On hummocks		In depressions	
	Total hits	Freq., per cent	Total hits	Freq., per cent
Eriophorum angustifolium	263	64.0	259	65.0
Carex pluriflora Hult.	169	45.5	94	33.5
Carex anthoxanthea Presl.	44	9.5		
Carex physocarpa Presl.			13	5.0
Scirpus caespitosus L.			38	6.5
Festuca altaica Trin.	49	8.0		
Calamagrostis canadensis (Michx.) Beauv.	9	2.5		
Equisetum palustre	55	13.5	41	15.5
Salix reticulata	118	36.0	2	0.5
Salix fuscescens And. var. *reducta* Ball	11	3.0	11	4.5
Salix sp.	12	5.0		
Moss	200	100.0	200	100.0
Menyanthes trifoliata L.	7	3.0	3	0.5
Andromeda polifolia	14	5.0	12	5.0
Swertia perennis L.	30	11.0		
Sedum roseum	23	7.0		
Sanguisorba sitchensis C. A. Mey.	96	28.5		
Thalictrum alpinum L.	42	13.0		
Erigeron peregrinus (Pursh) Greene	16	5.0		
Polygonum viviparum	12	5.5		
Viola adunca Smith	10	4.5		
Valeriana capitata	9	3.5		
Vaccinium oxycoccus	8	4.0		
Rubus stellatus Smith	4	1.0		
Pedicularis sudetica Willd.	3	0.5		
Caltha leptosepala	2	1.0		
Ranunculus sp.	2	1.0		
Ranunculus lapponicus L.	4	2.0		
Aster sp.	3	0.5		
Habenaria dilitata (Pursh) Hook.	2	0.5		
Pyrola secunda L.	2	0.5		
Trientalis europaea L. ssp. *arctica* (Fisch.) Hult.	2	0.5		
Total number of hits	1220		673	
Additional species in stand but not hit				
Anemone richardsonii	x			
Salix pulchra	x			
Polemonium acutiflorum	x			
Rubus arcticus L.	x			

would not immediately fill the part of the trench below the hummock. On the surface of the hummock or ridge was a layer of litter of tangled dead leaves, dead and living stems, living moss in the upper part and dead below, to a depth of 2.5 inches. Fine roots and willow stems were frequent in this layer.

Description of the soil profile under the ridge:

0–3.5 inches—black (2.0–2.5YR) muck, very spongy, very small amount of silt, very numerous roots and rhizomes, both fine and coarse.

3.5–24.5 inches—dark reddish brown (3/2–5YR), peat, very fibrous, live roots numerous.

24.5–25.5 inches—gray brown (5/2–10YR), silt, scattered light gray particles, roots numerous.

25.5–35.5 inches—dark reddish brown peat.

35.5–36.75 inches—very pale brown (7/4–10YR), silt.

36.75–37.75 inches—dark reddish brown peat.

37.75–38.75 inches—light gray (6/1–10YR), silt.

38.75–41.75 inches—dark reddish brown peat. Live roots were scarce below 25.5 inches, working depth about 24 inches, maximum depth could not be determined.

In the depression adjoining this ridge was a thin stand of plants, chiefly *Carex pluriflora, Equisetum palustre, Eriopho-*

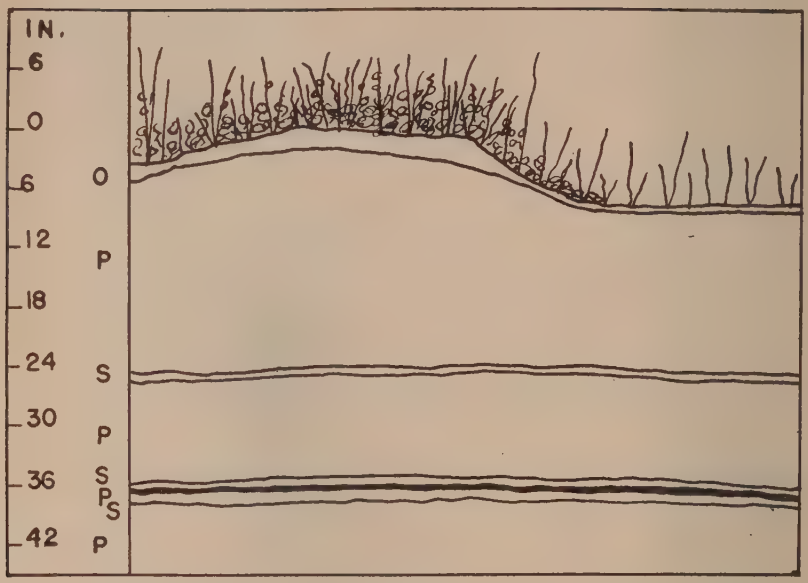

FIG. 7. Profile of a hummock and a hollow in an Alpine Sedge marsh, Craigie Creek, Talkeetna Mts. General easterly slope of less than 5°. Elevation about 3,100 feet. O = mucky organic layer, P = peat, S = silt. Chief species: *Eriophorum angustifolium, Carex pluriflora, Salix reticulata, Sanguisorba sitchensis,* and ground layer of mosses. July 26, 1949.

rum angustifolium, and mosses. The surface inch of the profile, under about an inch of water, consisted of the black leaves of sedges and other plants and of much brown or black moss with only some of the tips green. Below this was a layer, 2.5 inches thick, of partly decayed dark brown moss and some of the stems of plants which arose from the crowns located in the fibrous peat layer below. Beginning with the peat layer the horizons were the same as those below the ridge.

The general appearance of this stand on the gentle, water-logged slope, and the alternating layers of peat and silt indicated that solifluction has occurred here. No frozen ground was encountered as deep as the trench was dug, to about 42 inches.

SUMMARY

1. The vegetation and soil profiles are described in several solifluction and mound, or hummock, areas in Alaska, including Eagle Summit between Fairbanks and Circle Hot Springs, Mount McKinley National Park, Craigie Creek Valley in the Talkeetna Mountains, and in the vicinity of Kotzebue. Solifluction and mound areas are widespread in Alaska. The point-contact method was used to secure quantitative data on the degree of cover and the frequency, or dispersion, of the species in each stand that was studied.

2. The vegetation in these areas was dense, consisting of sedges as the most important species, with *Carex bigelowii* as the most abundant and widespread. Other important sedges were *Eriophorum vaginatum, E. angustifolium, Carex membranacea, C. misandra,* and *C. pluriflora.* Mosses, *Hypnaceae* chiefly, were abundant in most of the stands and *Sphagnum* spp. occurred in some. Species of *Salix,* particularly *S. reticulata,* were widespread. Heath plants, notably *Vaccinium vitis-idea, V. uliginosum,* and *Ledum decumbens,* were common. The forb with the

greatest frequency was *Polygonum viviparum.*

3. The ground in the solifluction areas was more or less hummocky and saturated with water. A layer of peat usually was found close to the surface, underlaid by a wet, fine silt horizon highly impervious to water. In most of the areas peat and silt layers alternated with increasing depth, the peat indicating former surface horizons. The depth to the frozen ground varied in relation to the angle and direction of slope, the amount of insulating plant cover, etc., from about 10 inches to about 25 inches, but in some sites frozen ground was not ecountered in late August, 1949, as deep as the trench was dug, *i.e.,* 46 inches.

4. The distribution of the roots is described in each profile. The working depth was usually at about 1.5 to 2.0 feet and the maximum depth slightly deeper. The root distribution was influenced greatly by the kind of soil material and the depth to the frozen ground.

5. The role of plants in the formation, building, and the disintegration of mounds is described. The invasion of plants into bare areas caused by various denudation processes appears to be rapid. This is effected mostly by vegetative means rather than by seeds.

6. Factors influencing solifluction and mound formation and mound movement are degree of slope, direction of slope, abundance of water at least during part of the year, upper ground horizons saturated with water, a fine silt or clay horizon below the saturated layer which has flow qualities, forces arising from freezing and thawing, an underlying layer of frozen ground or other hard material, and the presence of obstacles, such as boulders, ridges, or vegetation.

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NOTES AND COMMENT

RELATIVE ABUNDANCE OF SPECIES AND THE PYRAMID OF NUMBERS

The fact that some species are more abundant than others is so self-evident, even to the casual observer, that it is quite generally taken for granted and not considered worthy of further demonstration. In recent years, contributions by Fisher, Corbet, and Williams ('43), Williams ('44), and Preston ('48) have done much to renew an interest in the problems of relative abundance in nature and to increase our understanding of them.

It is obvious that differences in the relative abundance of animals are implicit in the gen-

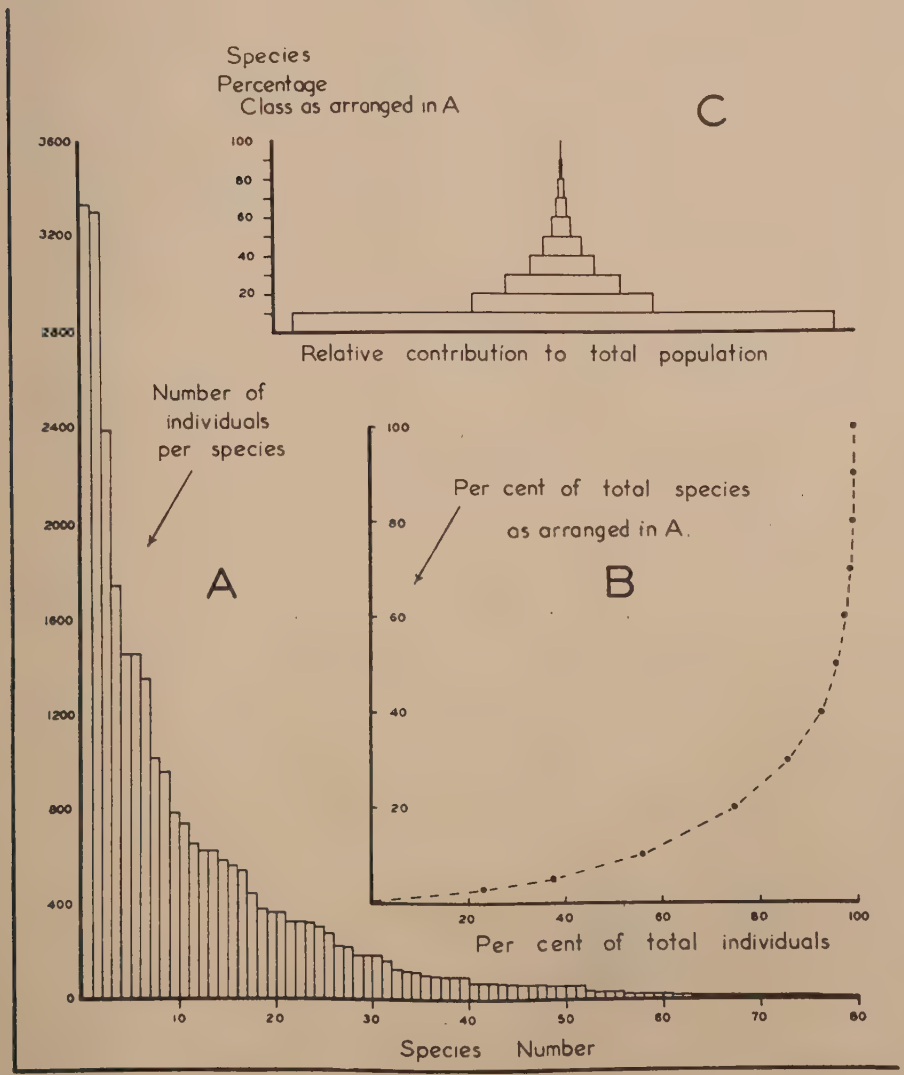

FIG. 1. Relative abundance of species in a population of breeding birds on a 17,000-acre tract. (Data from Saunders, 1936.)

eral concept of the pyramid of numbers as proposed by Elton ('27), along with differences in size and in food habits. Numerous diagrammatic illustrations of the pyramid have appeared in ecological literature, based either on grouping according to size or according to the trophic levels of the various species. Failure to find any examples based on relative abundance has prompted the writer to provide one. This is presented in the accompanying diagram (fig. 1), which is based on an estimate by Saunders ('36) of the numbers of pairs of nesting birds occurring on a 17,000-acre tract. If each of the 79 species is assigned a rank, and if the species are then arranged in order of decreasing numbers of individuals, we obtain a frequency distribution like that shown in A. The range of variation is considerable, with the most abundant species represented by 3,340 individuals and the least abundant by 2. If now we plot the per cent of the total number of species as arranged in A, we obtain an empirical curve like that shown in B. In this particular case, 5 per cent of the species account for 37.3 per cent of the individuals, 10 per cent of the species account for 55.9 per cent of the individuals, and 50 per cent of the species account for 96.0 per cent of the individuals. Finally, if the 79 species as arranged in A are now grouped in classes, each class representing an equal percentage of the total number of species, the relative contributions of each class to the total number of individuals can be shown graphically as in C. It is evident that this population pyramid has a broad base consisting of a few abundant forms.

These data were not derived from a single natural community but represent a combination of several communities. Nevertheless, there appears to be some correspondence between this arrangement of species according to relative numbers and groupings based on size or food habits. This shows most clearly in the upper part of the pyramid; the 23 (30 per cent) least abundant species included all of the hawks and owls present and only 2 species (purple finch, bobolink) that can be called plant-eaters. However, no great degree of conformity can be expected, since this population comprises a single taxonomic class and not an entire community.

Unfortunately, a complete count for every one of the species present in any community so far studied by ecologists is not yet available. Studies of relative abundance have been largely confined to particular taxonomic groups, for example, to series of snakes collected in Panama (Dunn, '49), and to Hemiptera and Lepidoptera taken at light-traps (Fisher, Corbet, and Williams, '43). These have shown relative abundance very much like that illustrated above, which is, after all, what one might naturally expect to find. There can hardly be many situations in which a majority of the species present live together in more or less equal abundance. Nor is it likely that one would find an evenly graded series running from most to least abundant. Differences in the numbers of those species which are intermediate in abundance would result in either a deepening or a flattening of the hollow curve shown in A and B, and no doubt each case shows its own variation. It seems likely, however, that the type of frequency distribution shown above is "normal" for many situations. If it is characteristic of component populations, it may also be characteristic of whole communities. Consideration of relative abundance, then, may be helpful in describing the structure of natural communities.

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DIFFERENTIAL FLOTATION AND DEPOSITION OF CONIFEROUS AND DECIDUOUS TREE POLLEN[1]

Introduction

This paper presents the results of a qualitative and quantitative study of the differential flotation of some coniferous and deciduous tree pollens. The study was prompted by reports of floating pollen drifted by the wind against the lee shore of a lake and the possible importance of this phenomenon to interpretation of pollen spectra.

Many attempts have been made to characterize the vegetation and thereby infer the climate from the evidence of fossil pollen preserved in peat and other sediments. This assumes a qualitative and quantitative relationship between the pollen produced by past vegetation and that recovered from contemporary deposits. To critical students of pollen analysis, it has long been evident that a pollen spectrum from bog or lake sediment does not present an absolute replica of past pollen rains. Following the release of pollen to the atmosphere by wind pollinated trees, many factors operate to destroy or redistribute the original components of a pollen rain and thereby distort the picture. The investigator is forced to base his conclusions as to the composition of the vegetation on those remnants from the pollen rain which are still available to him in his prepared samples. The following factors may bring about distortion.

a. Abundant pollen production by some species and meager production by others.

b. Position and number of tree species and their proximity to the receptive surface of the deposit forming area.

c. Climatic conditions, especially wind, at times of pollination.

d. Differential flotation on a water surface with sinking of most deciduous tree pollen and flotation of most conifer pollen.

e. Biotic and chemical destruction, the latter frequently selective in action, during processes of pollen fossilization.

f. Errors inherent in sampling methods.

g. Further pollen destruction by chemical preparation of the fossil material in the laboratory (usually selective).

For purposes of interpretation from pollen spectra, attempts must be made to compensate for factors which have produced differences between the original pollen rains and the pollen extracted from the sedimentary column. European workers have contributed heavily to our recognition of these factors, but in the writer's opinion, treatment of the problems arising from differential flotation of pollen is exceptionally inadequate.

Flotation of pollen had been reported as early as 1885 (Früh 1885), on Lake Constance, Switzerland, but it was not until 1931 that Wasmund ('31) clearly demonstrated in the Plöner Lake region of Germany the yearly occurrence of *Seeblüten,* composed almost entirely of conifer pollen, and noted its movement to leeward shores. The absence of deciduous tree pollens from drifting pollen had been reported earlier (Schröter und Kirchner 1896), and a controversy as to the significance of differential flotation to pollen analysis has subsequently developed. Only a few qualitative studies have been made of pollen flotation. Erdtman ('43) reports that in 1933 Pohl demonstrated that pine pollen retained its bouyancy for as long as four years. Wasmund ('31) observed that hazel and willow pollen sank in less than an hour when placed in an aquarium while spruce pollen had not sunk by the end of a month. The bulk of the work, however, has been based on field observation in which different levels of marine, lake, and peat sediments were sampled to discern whether differential flotation was responsible for shifts in pollen percentages. Lundqvist ('27) reported drift and concentration phenomena as factors to be reckoned with in analyzing lake sediments. Comparing samples taken near the shore of a lake with those taken at progressively greater depths farther from shore (samples were contemporaneous as to time of deposition), he found that the spruce pollen declined from 13 to 6% and the pine from 74 to 48%, while the birch pollen rose from 13 to 37% (it is not inferred that the birch pollen was numerically less abundant at any of the sampling sites). However, in an earlier study of a lake sediment by Lundqvist ('24), there was an increase instead of a decline in conifer pollen with increase in depth farther from the shore. Lüdi ('39), on the other hand, found little variation in the pollen spectra obtained from varying lake depths down to 39 meters in Lake Geneva. Erdtman ('21) noted a higher percentage of conifer pollen in materials from the surface of the bog mat in comparison to that found in surface sediment taken at a depth of ½ meter under water. Erdtman, at that time, felt that the two types of samples had not been deposited simultaneously. Most workers on small bogs reported few fluc-

[1] The writer is grateful to Drs. G. T. Jones, P. B. Sears, and F. O. Grover of Oberlin College for valuable discussions and assistance in preparation of this paper, to T. J. Cobbe for suggestions and preparation of the illustrative material, and to Dr. F. Foreman of the Geology Department for the loan of equipment and helpful criticism.

tuations in pollen spectra that could be attributed definitely to flotation.

Theoretically, sediments beneath open water in bog, lake, or sea would be nearly lacking in conifer, but proportionately rich in deciduous tree pollen; conifer pollen drifted to the shore of lake or sea might enrich sediments there, or be destroyed by physical, chemical, or biotic activities; or, in moving to the lee mat of vegetation in some bogs, the pollen might be caught, preserved and produce an over-representation at the contemporary face of the mat. If these distortions proved significant, interpretation of forest succession and climatic history would be open to this criticism. In spite of differential flotation, however, Erdtman ('43) concludes that, "Winds and currents carrying the surface water to the shore would tend to raise the conifer pollen percentage in the shore deposits compared with those which form in the center of the lake. This tendency, however, is not a regular one, since pollen washed ashore is often destroyed within a short time. As a rule, flotation does not constitute any serious source of error in pollen analysis. This may be indicated by comparing pollen spectra from sediments with those of contemporaneously formed peats."

This conclusion does not seem entirely reasonable to the present writer, because direct observation has shown that much of the conifer component of a pollen rain cannot be represented equally over wide areas of the sediments of lake and marine origin. If spectra from such sediments are comparable to those of peat bogs, the conifer pollen in the peat must also represent a distorted fraction of the original pollen rains. To obtain comparable net results is not to prove that, "As a rule, flotation does not constitute any serious source of error in pollen analysis," but rather that pollen spectra from either type of sediment are equally deficient in presenting us with a true picture of pollen rains. In all fairness to Erdtman's conclusion, it is noted that European workers have intensively studied many relatively small areas incorporating many types of sediments. With this massed data, variations and discrepancies in pollen spectra can be discovered and discounted in the formulation of interpetations. The mechanics of flotational effects and the reasons for comparable spectra, however, are not solved by such a method. Furthermore, we are presented with conflicting evidence, namely, bouyancy of conifer pollen, and its presence in sediments formed under open water. One of the necessary approaches to an attack on these problems involves determination of the relative degree of flotation of various tree pollens. Experiments were therefore performed with beakers and two tanks of a type used in sedimentation studies. While natural conditions are by no means duplicated, it is felt that significant results were obtained.

Methods

Preliminary observations

In the spring of 1949, tree pollens (and pollen of one shrub, *Corylus*) were collected by gently tapping pollen from the fresh flowers or cones onto the water surface of 250 and 850 ml beakers. The time in which all, or a part, of the pollen sank was noted (table I). Judging from the behavior of *Pinus banksiana* and *Fraxinus americana* pollens, it cannot be generalized that all of the pollen of a species without bladders will sink rapidly while all grains of those with bladers will float.

Table I. *Differential flotation of fresh pollens on water-filled beakers*

Species	Per cent sinking (approximate)	Time
Juniperus virginiana L.	95–100%	5 min
Larix decidua Mill.	95–100%	5 min
Corylus americana Walt.	95–100%	5 min
Betula papyrifera (Marsh.) Spach	95–100%	5 min
Betula populifolia Marsh.	95–100%	5 min
Quercus palustris Muench.	95–100%	5 min
Quercus macrocarpa Michx.	95–100%	5 min
Populus grandidentata Michx.	95–100%	10 min
Fraxinus americana Lamb.	50%	12 hrs
Pinus banksiana Lamb.*	30%	1 hr
Pinus resinosa Ait.*	5%	24 hrs

* Grains with air bladders.

Detailed experiments

To obtain more natural surface tensions (surface tensions would be high on the limited water surface of beakers), sedimentation tanks of two sizes were used.

The first tank measured 6 × 6 × 2.5 ft. (fig. 1), and the second, 15.25 ft. × 19 in. × 17.5 in. (fig. 2). One hundred deposition jars were used which stood 4.25 in. high with an inside diameter of 1.8 in. To the lid of each jar was cemented a 2 ft. length of very fine wire. The lids were placed alongside their respective jars, permitting the latter to be capped with a minimum of disturbance in the water.[2]

Experiment 1. Comparison of rates of sinking of pine and oak pollens in the absence of wind.—In the 6 × 6 ft tank, the water level was brought to a depth of 17 in. following the place-

[2] The water level was of such height that the tips of the wires protruded a few inches above the surface when the tanks were ready for use, and a small amount of pollen tended to collect around the wires but since the capping wires were not over the open mouths of the jars, this was considered to be an insignificant source of error.

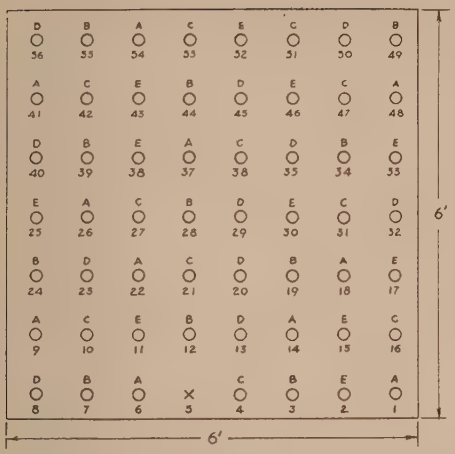

FIG. 1. Tank used to study deposition rates of pollens in the absence of wind. Top view of tank with jars in place. "A" jars capped after 10 minutes; "B" after 1 hour; "C" after 12 hours; "D" after 48 hours; and "E" after 120 hours.

ment of jars and caps. In this and other tank experiments, two days were allowed for the water to attain room temperature to insure against convection currents. Five grams of fresh *Quercus palustris* and four grams of *Pinus resinosa* pollen were mixed and tapped from a packet over the water of the first tank (fig. 1). After 10 min., the "A" bottles were capped; after 1 hour, the "B" bottles; after 12 hours, the "C" bottles; after 48 hours, the "D" bottles; and after 120 hours, the "E" bottles were capped. The caps were then tightened, the jars removed and placed upright in cardboard containers to await analysis (3–5 drops of toluol were later added to the contents of each jar).

Expression in per cent of the amounts of pine pollen that sank required a rough approximation of the number of pine and oak grains in a gram of each. A dilution method was used for this purpose. A dilution of 1 to 700,000 was ultimately obtained, and the results from 5 samplings of the oak and pine solutions gave an average of 129 grains for oak and 79 grains for the pine.[3] The final computations for the number of grains in a gram gave an approximation of 90,300,000 for the oak, and 54,600,000 for the pine.

The following procedure was used for counting the grains found in the deposition jars. About ⅔ of a jar's contents was decanted; 50 cc more water was removed from the jars by slowly pipetting at the surface (these operations did not visibly disturb the pollen resting on the bottom). Jars were shaken and the remaining liquid (about 80 cc) was poured into centrifuge tubes. After successive concentrations, all the pollen sediment was finally collected in one tube. 75–90% of this pollen sediment and a drop of glycerine were placed on a slide, and the pollen counted.

The pollen had not been spread on the water with perfect evenness, so a comparison of the number of pollen grains that fell in each jar would be meaningless. The beaker tests, however, indicated that all of the *Quercus palustris* pollen sank quickly, and if pine and oak grains were thoroughly mixed in known proportions, the oak pollen count in each jar could be taken as the base figure for computing the percentages of pine pollen that sank. Twenty-five jars were chosen for analysis to represent 5 widely scattered deposition points in each of the 5 groups "A," "B," "C," "D," and "E." The percentage of pine pollen that sank was derived as in the following example. If 4,000 oak and 100 pine grains were counted from one of the jars, 2×100 would be divided by 4,000 giving 0.05 or 5% (pine count was doubled since approximately ½ as many pine as oak grains were used).

Results: Table II presents a condensation of the results. In the first column are listed the 5 specific jars of each time series (see fig. 1 for jar distribution). The second column gives the time of exposure before capping; the next column, the extreme counts of oak grains in jars of each series; the fourth column, the extreme counts of pine pollen; the fifth column, the extremes of the derived percentages of pine grains in a series; and the last column, the average percentage of pine grains that sank in the jars of a series. It should be pointed out that the proportion between oak and pine pollen grains is desired rather than variations between total numbers of grains that sank. That an average of about 4% of the pine pollen fell in the first

[3] Single one-gram samples of *Pinus resinosa* and *Quercus palustris* pollen were placed in flasks containing one liter of water. After vigorous shaking, 10 cc were immediately pipetted from the middle of the suspension. The 10 cc in turn were placed in 990 cc of water and again vigorously shaken. Three drops from this last solution were pipetted out on a slide and all the grains present were counted. Dilutions were $1 \times 100 \times 7{,}000 \times 129$ for oak and $1 \times 100 \times 7{,}000 \times 79$ for pine pollen (3 drops from the pipette used equalled 1/7 of a cc). Whether the pollen is of the floating or sinking type, a more or less homogeneous suspension is temporarily possible; it is not known to what extent strong wave action may bring this about in nature also. The author's observations of fresh pollen in a water medium suggested that the specific gravity in water of floating or sinking pollen types is very nearly 1.

TABLE II. *Time period and percentages of pine grains that sank*

Sample jars	Time of jars exposure	Oak grains extremes*	Pine grains extremes**	Per cent pine extremes	Average per cent pine
9, 18, 22, 37, 54	10 mins (Group "A")	1,980–4,805	32–85	3.2–4.8	4.0
3, 34, 44, 49, 55	1 hr (Group "B")	2,885–8,670	42–204	2.9–5.3	3.9
21, 27, 31, 36, 42	12 hrs (Group "C")	2,730–7,815	55–173	3.3–5.6	4.2
8, 13, 20, 45, 56	48 hrs (Group "D")	2,265–6,020	63–184	3.6–9.1	6.1
2, 11, 25, 30, 33	120 hrs (Group "E")	3,705–7,480	177–307	8.2–10.0	8.8

* Total oak grains counted: 114,500.
** Total pine grains counted: 3,125.

10 min., with little additional settling until after the 12th hour, indicates more than one set of factors are operative in settling of some pollen of this pine species.

Experiment 2. Deposition of oak and pine pollen under simulated wind conditions.—The second tank (fig. 2) was equipped with a canvas wind tunnel and a two-speed fan. Bottles and caps were arranged as shown, the hood adjusted over the stays, and the platform and fan placed in position. The platform served the purpose of protecting the surface of the water near the base of the fan to prevent excessive agitation in that area. The approximate wind velocity near the fan and at the end of the tunnel was then determined. At low speed of fan, the velocity averaged 740 ft. per min. 15 in. in from the fan end of the tank. At the far end of the tank, the average velocity was 340 ft per min. The construction of the tunnel unfortunately permitted air leakage, but it is thought that useful evidence was obtainable despite the lack of data on the precise wind velocity at points throughout the length of the tank.

A mixture of two grams each of *Pinus resinosa* and *Quercus palustris* pollens (approximately 110 and 185 million grains, respectively), was scattered in a strip across the surface of the water 6 inches off the edge of the platform while the fan was not running. The fan was immediately turned on low speed. The air-flow produced a slight rippling of the water surface, and the pollen exhibited a windrow effect as it moved down the tank. The fan was turned off

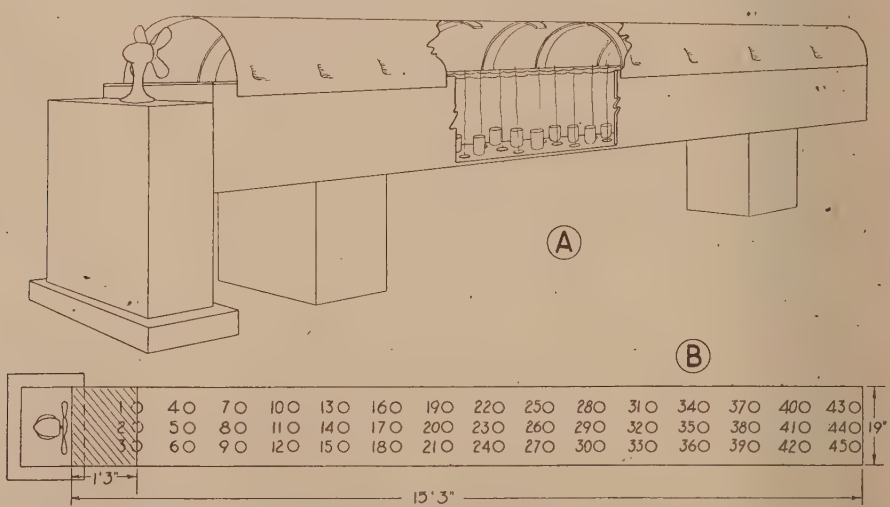

FIG. 2. Wind tunnel and tank. **A**: Three dimensional side view and cut away of tank used for simulated wind conditon. **B**: Diagram of the same tank with jars in place, viewed from above.

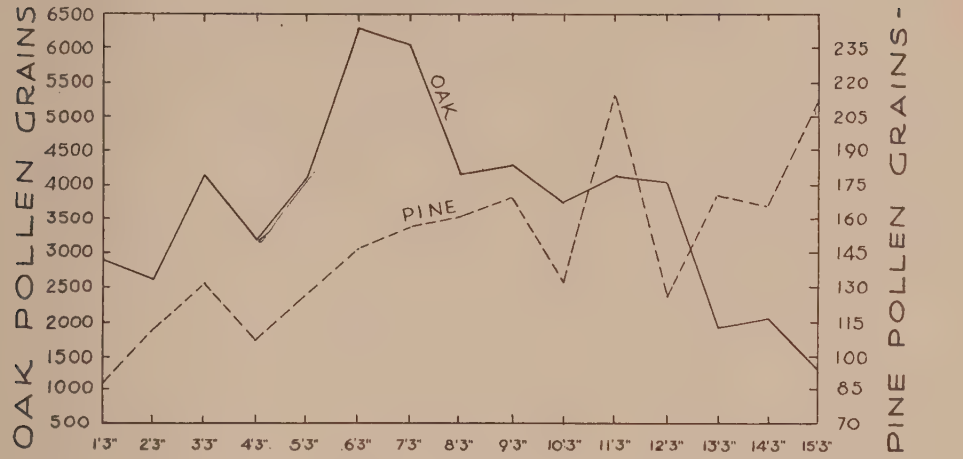

FIG. 3. Depositon of *Quercus palustris* and *Pinus resinosa* pollen at the collection points. Abscissa: the distance of each collection point from the fan end of the tank. Ordinate on the left repesents the number of oak grains that sank, that on the right, the number of pine grains that sank. Total oak grain count: 109,285; total pine grain count: 4,194.

after 70 sec at which time the pollen had approached within 5 inches of the far end of the tank. The bottles were quickly capped beginning with those nearest the fan. While this was in process, floating pollen was observed to be caught and held by the meniscus along the edge of the tank. Four samples were taken from this floating pollen, and examination showed it to consist of pine grains with a very rare inclusion of oak pollen.

Results: The results are presented in figure 3 where the abscissa is scaled to represent the length of the tank in 12-inch units, and the ordinates to represent the numbers of oak and pine grains that sank. The maximum settling of the oak grains took place by the time the pollen mass had drifted half the length of the tank, indicating that a short period of wetting was followed by heavy settling. The decline in the number of settled oak grains as the far end of the tank was approached is assumed to be due to the progressively reduced amount of oak pollen available. The increase of the pine pollen in jars towards the far end of the tank might have been due to slower wetting than that of oak combined with the lessening wind velocity and extra time to sink in the few minutes in which the bottles were being capped.

Experiment 3. Rate of drift of pine and oak pollen at winds of two velocities.—After removal of bottles, emptying, and refilling the tank, two grams of *Pinus resinosa* pollen were placed as specified in the preceding experiment.

Results: The fan was turned on low speed (740 to 340 ft per min), and the average time for three trials in which pollen reached the far end of the tank was 69 sec. At high fan speed with an average velocity of 920 ft per min and 415 ft per min at the fan and far ends of the tank, respectively, the pine pollen travelled the distance in 55 sec. Two grams of oak pollen were similarly treated, but almost all of it sank before reaching the far end except for a few grains found clinging to anther fragments. In this last set of experiments, the distance travelled was about 13.4 ft. At low speed of fan, the air velocity was about 8.4 mph near the fan and 3.9 mph at the far end. The speed of the pollen was 0.13 mph. It is evident that a pollen mass may drift rapidly across the surface of a body of water. It is reasoned, however, that the rate of increase in the speed of drift of a pollen mass would not remain proportional to the rate of increase of the wind velocity as drag and wave action factors became more pronounced.

Experiment 4. Sinking of pine pollen in relation to its grain bladder sizes.—Erdtman ('43) presents some of the investigations of Pohl and other workers on the specific gravities of conifer and deciduous tree pollen, but their computations concern only the theoretical rates of settling in air of air-dried pollen. Other factors than specific gravity must be involved in the floating of some of the pollen of a species and the sinking of the rest. One factor to consider is the difference in the size of the grain body in proportion to the size of its bladders. A size-frequency study was therefore made of 150 grains of *Pinus resinosa* pollen collected from the surface of tank 1, and of 150 grains that sank in the collection jars (both samples were

TABLE III. *Summary computations of sizes of floating and sinking* Pinus resinosa *pollen*

Dimensions measured*	GL	GL′	GD	GD′	WD	WD′	WB	WB′
Extremes	35.2–49.6	30.4–51.2	22.4–36.8	20.8–38.4	16.0–22.5	11.2–22.4	22.4–32.0	17.6–30.4
Mode	41.6	43.2	30.4	30.4	20.8	16.0	25.6	25.6
Mean	41.507	41.633	30.24	28.933	20.500	16.260	26.7	24.473
Stand. Dev.	1.44	2.55	1.54	2.27	1.25	1.31	1.26	1.55
Stand. Err.	.118	.207	.126	.185	.102	.107	.102	.127

* GL, GD, WD, WB; measurements of floating grains in microns. GL′, GD′, WD′, WB′; measurements of grains that sank in microns.

taken at the end of experiment 1). Four measurements were taken from each grain following Cain's ('40) description of grain length (GL), grain diameter (GD), wing diameter (WD), and wing breadth (WB).

Results: The significant features of the measurements are evident in the comparison of the grain lengths (GL) and the wing diameters (WD). The pollen that remained afloat (table III) shows a mean for GL that closely corresponds with that of the grains that sank, but in the former, the standard deviation was 1.44, and in the latter 2.45. The mean wing diameters for those that floated was 20.50 μ and for those that sank only 16.26 μ. The standard deviations for the two were 1.25 and 1.31, respectively. Grain diameters were somewhat comparable in their means, but the sizes of those grains that sank had a standard deviation of 2.27 as compared to 1.54 for those that floated. These figures indicate that grains with small wing diameters comprised the majority of those that sank. Whether or not smaller wings were unable to support their grains at the surface, or were less able to retain their air due to structural deficiencies was not ascertained.

General Discussion

Buoyancy of the pollen

On the basis of the beaker tests, one cannot assume that all pollen grains with bladders will float while others will sink. The evidence only seems to indicate that the majority of the grains with bladders (most conifers) will float, while the majority of those without bladders (deciduous trees) will sink. The proportion of grains which will float to those which will sink is species specific, as suggested by *Fraxinus americana* of the deciduous tree group and *Pinus banksiana* of the conifer group, but the present study is not extensive enough to discover whether the actual percentages remain constant in point of time and geographical range. Under field conditions, the behavior of pollen will probably be affected by the biotic and chemical qualities of the water upon which it settles and possibly also on wave action. At any rate, a solution is proposed for the problem of the presence of buoyant conifer pollens in lake and sea sediments. Beaker and tank experiments revealed the rapidity with which *Quercus* pollen sinks. Such rapidly sinking pollen types would presumably be found in underwater sediments as evenly distributed as when they fell upon the surface of the water (excluding complications induced by sedimentary petrologic phenomena and accidents of preservation).

The experiments substantiate field observations on the ease with which conifer pollen drifts across a body of water and concentrates at the lee shore. With a breeze of less than 8 mph, conifer pollen may be expected to drift at the rate of between 0.1 and 0.2 mph. Assuming a higher rate of pollen drift with increased wind velocities, a considerable distance could be covered by a pollen mass in a relatively short period of time.

Explanatory hypothesis

From the size-frequency studies (table III) of pine grains that sank and those that remained afloat, it seems justifiable to conclude that grains with undersized bladders (or small in comparison to the body) are more prone to sink. The grain lengths (GL) of grains that floated ranged from about 35 to 50 μ (standard deviation of 1.44), while those that sank ranged from 30 to 51 μ (standard deviation of 2.55). The greater deviation encountered in the size of the grains that sank has import for determinations of species of *Pinus* by size-frequency studies of their fossil pollen (Cain '40, and Cain & Cain '48). A few μ plus or minus is often sufficient to place a grain in a size category denoting a species which it may or may not represent. Fossil pollen removed from sediments which originally had been deposited under open water, would thus present less reliable curves

for the species involved than that from differently formed deposits.

A number of factors may be involved in the sinking of pollen. Both tank experiments with deposition jars indicated an initial deposition of part of the *Pinus resinosa* pollen while further contact with water was necessary for additional settling. Sequences of sinking are surmised as follows. Grains that immediately settled were probably those whose bladders, perhaps through some structural defect, permitted rapid replacement of their air with water. Pine pollen settling later perhaps became wetted (dependent on differences in the amount and quality of water-resistant substances on their bladders' surface), and sank if their bladders were relatively too small to support the grain body at the surface. A third group would settle upon wetting followed by expansion of grain body and bladder walls and by germination, or by rupture of some weak spot on the bladder. Replacement of the air by water might take some time and settling of a small percentage of the grains could continue for many hours. Evidence furnished by the experiment in the tank (fig. 1) does not indicate whether deposition ceased sometime between the 48th and 120th hours or continued beyond the conclusion of the experiment. The number of pine pollen sinking per hour, however, obviously declined sometime after the 48th hour. It is assumed that about 90% of the *P. resinosa* pollen would have remained afloat indefinitely (a thick pollen scum was observed on the tank's surface 5 weeks after the conclusion of the experiment). The above points are based in part on an examination of the pollen that floated and that which sank. Floating grains almost invariably showed both bladders still filled with air. Grains that sank had both or sometimes one bladder filled with water. After centrifuging a sample of pollen that had remained afloat, almost all grains had their bladders filled with water. Whether wave action on a sandy beach or even on open water might have a similar effect by facilitating wetting and sinking is unknown.

Of questioned validity are the conclusions drawn by Cain and Cain ('48) from the large percentage of small sized pine pollen found in the bottom sediment of Sodon Lake. Subsequent levels had fewer grains of this sort. The Cains suggested that, "*P. Banksiana* had its period of greatest relative abundance immediately after the spruce-fir period at the bottom of the sediments." This might be ecologically sound, but the pollen measurements alone do not prove it. If the present writer's *P. banksiana* pollen samples were typical (approximately ⅛ sinking in 1 hour in beakers), proportionately more pollen of that species would be deposited in bottom sediments of a lake than pollen of *P. resinosa* (approximately 4% sinking in 1 hr). This would be true even if the pollen of the latter species was actually in greater abundance on the lake's surface. If *P. strobus* pollen also proved more buoyant than *P. banksiana* pollen, trees of the former, as well as those of *P. resinosa,* might have been abundant in the area even though their pollens would be largely absent in the bottom sediments.

It has not been ascertained whether the number of grains that sink will vary with the physiologic, genetic, and environmental factors acting in and about the plant at the time of pollen production, and such studies should of course be made.

Relation to pollen analysis studies

The writer is not ready to accept the premise found in the literature, that no evident source of error is involved in pollen analysis due to differential flotation of pollen. The gradual settling of a portion of *P. resinosa* pollen and other conifer pollens that might behave in a similar manner would progressively increase the pollen concentration in sediments beneath waters across whose surfaces the pollen mass was drifting. In bogs with some open water, at present or at previous stages in their development, the pollen that drifted to the edge of the shore vegetation theoretically would be caught and preserved as the grains were worked into the edge of the vegetation at and just below the water's surface. One should not expect a pollen spectrum from such material to agree with that from ooze formed under open water, nor with that from samples taken from the surface of the mat. Judging from the present study, one would conclude that pollen spectra derived from sediments formed under open water are probably distorted, and it would seem that if comparability with spectra from peat accumulations does occur, the depositional and preservational mechanisms in the latter have somehow brought about equivalent distortions.

The above statements may readily be criticized on the basis that the field of pollen analysis is concerned only with interpreting broad and generalized shifts in pollen percentages, and that a close examination of a limited portion of the pollen spectrum would therefore be pointless. Such an assumption is no longer valid as reference to the trend of studies in Europe indicates. Much effort is being directed to discovering and interpreting minor fluctuations of pollen percentages in the pollen spectrum. Recurrence surfaces in sediments indicating changes in water relationships and the attendant shifts in pollen content have received considerable attention by von Post and others. The possibilities of obtaining reliable data of minor climatic rhythms of relatively short duration led von Post ('46) to state, "This much, however, is made clear by this diagram and by

many other observations: the detailed course of the climatic changes has been exceedingly complicated, but beyond the intricate picture we catch a glimpse of a mathematical law which perhaps will ultimately appear quite simple."

The present writer considers the phenomenon of differential flotation of particular concern to investigations in this country where so many of the sediments have been deposited in an open water stage. Rigg ('40) noted that raised sphagnum bogs (where no flotation effects are possible) are rare in North America generally, though common in eastern Canada, eastern Maine, and along the Alaska coast. American investigators are thus forced to deal largely with former glacial lakes or shallow water-filled depressions, and in some areas, chains of lakes initiated by beavers (Manville '49). Some of the pollens now preserved in the sediments on such sites were affected at one time or another by flotation (as long as open water was present). Due to these circumstances, other types of sediments in adjacent localities have not always been available for comparative purposes. It is noted that Godwin ('45) made extensive correlations between pollen spectra from carefully selected coastal peat beds of the North Sea region. Many of these deposits were of the raised bog type (no flotational effects possible), with sedimentary layers of temporary marine invasions further aiding his correlations. Work in Sweden, of course, has permitted pollen spectra comparisons between "spring bogs," raised bogs, flat or lowland bogs, and lake and marine sediments. In order to develop new approaches which will distinguish between discrepancies in pollen spectra due to distortions resulting from flotation, preservation, etc., and those that truly indicate short climatic rhythms, much critical and intensive work must be performed on problems particular to North American deposits. Until this is done it is doubtful whether we can safely begin to follow the present trend of European investigations. It is hoped that this study of differential flotation is a step in that direction.

Summary

The buoyancy of a number of conifer and deciduous tree pollens was tested in beakers and two sedimentation tanks. The majority of those deciduous tree pollens tested sank rapidly while bladder-equipped conifer grains tended to float. The degree of buoyancy in both types was indicated to be species specific. In a tank equipped with fan and wind tunnel, the ease with which a floating pollen mass is drifted checked with field observations of Wasmund and other European workers. The sinking of *Pinus resinosa* pollen was computed to be 4% during the first 10 min. followed by little sinking for the next 12 hours, but averaging a total of 8.8% by the end of 120 hours. Size-frequency studies of those grains that floated as compared to those that sank indicated that grains with small bladders compared to their grain sizes comprised many of those that sank.

It was concluded that the observed sinking of a small percentage of *Pinus resinosa* and like-behaving conifer pollens could account for their presence in deep-lying lake and marine sediments despite their reported buoyancy. The prevailing opinion, that differential flotation is not a serious source of error in pollen analysis, is based on reports that pollen spectra obtained from variously formed peats are comparable with those from lake and marine sediments. The interpretation of these data is questioned since the pollen spectra from lake and marine sediments may be distorted by differential flotation, and if there is a real agreement with spectra from bogs the latter must also be distorted by some other compensating circumstance.

In size-frequency studies of fossil pine pollens, there is a possibility that the sizes of grains deposited in sediments formed beneath open water are more variable than those found in sediments not so formed. The marked difference in the degree of flotation between pollens of some pine species indicates that the relative abundance of their pollen in bottom sediments would not show the original relationships that existed between their respective pollen rains.

Present efforts to detect short climatic rhythms in pollen spectra demands closer attention to differential flotation of pollen. This is especially true in North America where the majority of sediments are of glacially formed bog-lake types with few differently formed deposits to serve for comparative purposes.

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INFLUENCE OF THE INTERACTION OF ENVIRONMENTAL FACTORS UPON THE IMMATURE STAGES OF THE RICE WEEVIL[1]

In recent years Birch ('45a, b, c) conducted experiments regarding the influence of varying environmental conditions upon the development of the rice weevil. However, little information is available concerning the effect of the interaction of the different environmental factors upon the development of the egg, larval instars, prepupa and pupa of the rice weevil. In this investigation a study was made of the influence of temperature, relative humidity and the moisture content of food upon the development of the immature stages of the weevil, *Sitophilus oryzae* (L.).

MATERIALS AND METHODS

Unpolished rice in equilibrium with a relative humidity of 65 and 84 per cent which resulted in a moisture content of 12.6 and 15.1 per cent respectively was used. Constant relative humidities were maintained by using sulphuric acid solutions in water. The moisture content of the rice was calculated on the basis of wet weight.

Small quantities of each sample were placed in separate culture bottles (approximately 50 ml. capacity) and 30 fertilized females were introduced into each bottle which then was covered with a light muslin cloth. These cultures were placed in cabinets of constant temperature of 26.6°, 30°, 32° and 35° C. Females were removed from each culture after a 24 hour oviposition period. Throughout the experiment, a sample of more than 20 grains from each culture was dissected daily in order to determine the stage of weevil development. The different larval instars were distinguished on the basis of the width of the head capsules. Dissections of the grain from cultures having a moisture content of 12.6 per cent were not made for the prepupal and pupal stages because the proportion of the infested grain in these cultures was very low. In the other cultures dissections of the grain were continued until the pupae completed their development.

RESULTS

The experimental results obtained are summarized in table I. Of the three temperatures used eggs hatched in the shortest time at 32° C in rice having a moisture content of 15.1 per cent. Within the developmental range eggs hatch more rapidly at higher temperatures than at lower temperatures. A difference of 2° C does not affect the rate of development of the egg in rice of 12.6 per cent moisture whereas in rice of 15.1 per cent moisture eggs hatch faster at 32° C than at 30° C. In general, however, eggs hatch faster in rice of higher moisture content. At a temperature of 35° C no eggs hatched at any moisture content of the rice.

The influence of temperature and moisture content of rice upon the development of different larval instars is not uniform. The duration of the first larval instar is shortest at 30° C in rice of 15.1 per cent moisture and at 30° C in rice of 12.6 per cent moisture. The rate of development of other larval instars also varies due to the interaction of temperature and the moisture content of the food.

Different larval instars complete development more rapidly in rice of 15.1 per cent moisture than in rice having a moisture content of 12.6 per cent. The influence of temperature upon the development of the larval instars, on the other hand, is irregular and varies with different temperatures at different moisture contents of food. However, the shortest time

[1] Acknowledgments are made to Dr. A. E. Michelbacher for his advice during the investigation. The author is indebted to Professor E. O. Essig for his help and provision of facilities. Gratitude is expressed to Miss M. Maxine Moeller for her valuable help.

TABLE I

Temperature ° C	Relative humidity, per cent	Moisture content, per cent	Average number of days to complete development							
			Egg	Larval instar				Prepupa	Pupa	Egg to prepupa
				I	II	III	IV			
26.6	65	12.6	6	6	5	6	8	—	—	31
	84	15.1	5	3	4	3	5	2	6	20
30.0	65	12.6	5	6	4	4	5	—	—	24
	84	15.1	4	2	3	3	4	2	4	16
32.0	65	12.6	5	5	6	6	7	—	—	29
	84	15.1	3	4	3	4	4	2	5	18

for the complete development of the larva is found to be at 30° C in rice of both moisture contents.

The data on the development of prepupae and pupae in rice of 12.6 per cent moisture are not available. The duration of prepupa is very short and the rate of development at different temperatures is the same in rice of 15.1 per cent moisture.

The pupa develops rapidly at 30° C and above this temperature development is retarded.

SUMMARY

The temperature and the moisture content of the food interact in their influence upon the development of the immature stages of rice weevil.

Eggs hatch in the shortest time at 32° C in rice having a moisture content of 15.1 per cent but this period is the same at 30° and 32° C in rice of 12.6 per cent moisture. No eggs hatched at 35° C in rice of both moisture contents.

The rate of development of the different larval instars is not uniform and varies with different temperatures and also with different moisture contents at the same temperature. However, the larva develops in the shortest time at 30° C, the total period from egg to pupa also being shortest at this temperature.

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STABILITY AND ZONATION OF CHARACEAE[1]

The distribution of the Characeae has generally been conceived to be as unique as the numerous other features of these plants. They are often thought of as being markedly transitory plants that occur suddenly in a given habitat and disappear equally as suddenly a year or two later. This observation is an accurate one, and it certainly can be confirmed by repeated reports and investigations. That this is not universally true is doubtlessly recognized at least by those who have had occasion to observe aquatic habitats over a number of years. It was felt that a specific statement was needed in this regard, together with supporting evidence.

Since 1946, the writer has had the opportunity to make a number of repeated field observations while undertaking a taxonomic study of this group of plants. These notes, together with data from herbarium studies, seem to offer sufficient information for presentation at this time. The nomenclature employed for these plants is that which he has followed in his

[1] Read in part before the Phycological Society of America, December 27, 1949, New York.

TABLE I. *Transient occurrence of Characeae in a small pool as indicated by changes in vegetation in Chara Haven, Oyster Pond, near Woods Hole, Mass.*

Plant	Coverage					
	1946		1947	1948	1949	
Chara delicatula	0	++	+++++	++	+	0
Chara Braunii	0	++	+++	0	0	0
Najas flexilis	0	+	+++	+++++	+++++	+++++
Potamogeton sp.	0	0	0	+	++	++
Algal slime	0	0	0	*	**	***

Key to symbols:

+ = 1/10 total area.
* = relative density.
Double columns in 1946 and 1949 indicate early and late summer conditions, respectively.

TABLE II. *Degree of stability (i.e., minimum period of occurrence) of Characeae in certain habitats as indicated by the years over which herbarium records are known*

Station	Species	Herbarium records	Stability (years)
Sheep Pond Cuttyhunk, Mass.	*C. Braunii*	W. R. T.—1925	1
	C. delicatula	W. R. T.—1932 —1934 —1945 R. D. W.—1947	15
	N. flexilis	W. R. T.—1932	1
Put-in-Bay South Bass, Ohio	*T. intertexta*	A. J. P. —1898	1
	C. Braunii	A. J. P. —1898 R. D. W.—1947	49
	C. contraria	A. J. P. —1898 R. D. W.—1940 —1941 C. A. V. —1949	51
	C. Macounii	A. J. P. —1898	1
	C. keukensis	A. J. P. —1898	1
	C. compacta	A. J. P. —1898	1
Watch Hill Rhode Island	*C. canescens*	W. A. S. —1889 —1892 R. D. W.—1948	59
	C. aspera	W. A. S. —1892 E. A. P. —1948	56
Chara Pond Cape Cod, Mass.	*C. canescens*	F. S. C. —1882 J. M. F. —1925 H. T. C. —1945 R. D. W.—1947 —1948 —1949	67
	C. delicatula	W. R. T.—1937 R. D. W.—1947 —1948 —1949	12
	C. Braunii	B. D. R. —1941	1

Collector name abbreviations: A. J. P.—*A. J. Pieters;* B. D. R.—*B. F. D. Runk;* C. A. V.—*Core, Anderson* and *Verduin;* E. A. P.—*E. A. Palmatier;* F. S. C.—*F. S. Collins;* H. T. C.—*Hannah Croasdale;* J. M. F.—*J. M. Fogg, Jr.;* R. D. W.—*R. D. Wood;* W. A. S.—*W. A. Setchell;* W. R. T.—*W. R. Taylor.*

earlier taxonomic studies ('47, '49), and descriptions of the plant materials as interpreted by him can be found in those references. Determinations of plants other than Characeae were provided by Dr. E. T. Moul of Rutgers University, and the nomenclature for such forms follows Fassett ('40).

Characeae as a Transient Vegetation

One small pool has been under observation by the writer for four years (table I). Chara Haven, a pool adjacent to the seaward side of Oyster Pond, near Woods Hole, Massachusetts, is about twenty feet long by six feet wide and eighteen inches deep. It was apparently formed in some manner unknown to the writer during the winter of 1945–6. In early summer of 1946, it was "sterile," but by late that summer had been invaded by an extensive growth of *Chara delicatula* Ag., *C. Braunii* Gm., and a little *Najas flexilis* (Willd.) Rostk. & Schmidt. In the summer of 1947, all three species increased in area covered. In 1948, *C. Braunii* disappeared and *C. delicatula* was markedly reduced; whereas, the Najas increased and *Potamogeton* sp. had appeared. In early summer of 1949, the *C. delicatula* was nearly gone. By the end of the summer, the Charas had disappeared entirely and Najas, Potamogeton, and Typha were well established. Thus, the Characeae were quite transitory, and the succession in this habitat was relatively rapid.

Characeae as a Relatively Stable Vegetation

Absolute proof of continued occurrence of a given species of Characeae in a given habitat over extended periods of time is extremely difficult to obtain, since so few workers have been sufficiently interested in the group to have continued observations for more than a few years in any one locality. Evidence which, although imperfect, provides material basis for

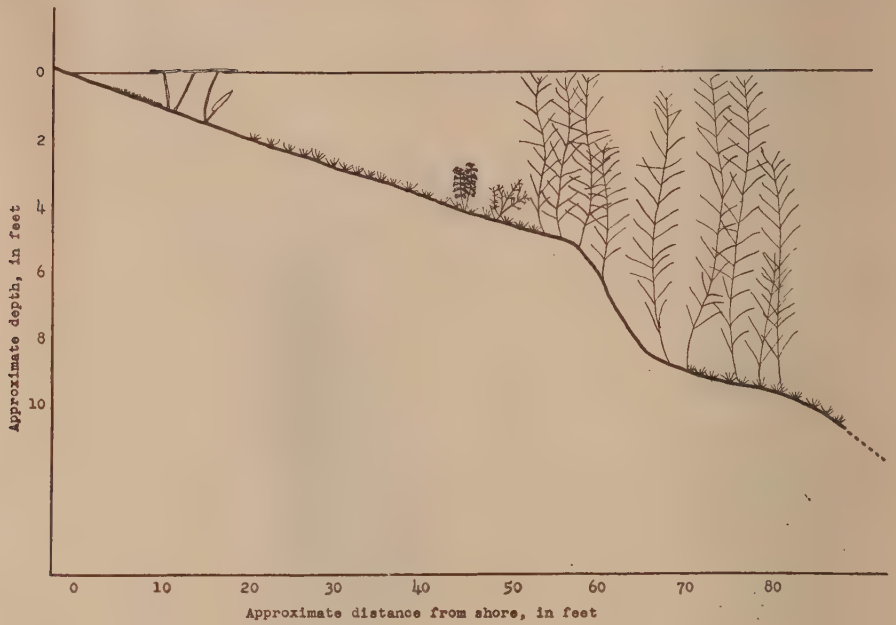

FIG. 1. Vertical zonation of aquatic plants in Weeks Pond, Falmouth, Mass., August, 1947, with special reference to Characeae. Major constituents: 0–1 ft., *Gratiola lutea;* 1–3 ft., *Nymphaea odorata;* 3–5 ft., *Nitella transilis* (occasional *N. megacarpa*), *N. flexilis,* and *Chara Braunii;* 5–9 ft., *Potamogeton* sp.; 9–? ft., *Nitella transilis* and *Potamogeton* sp.

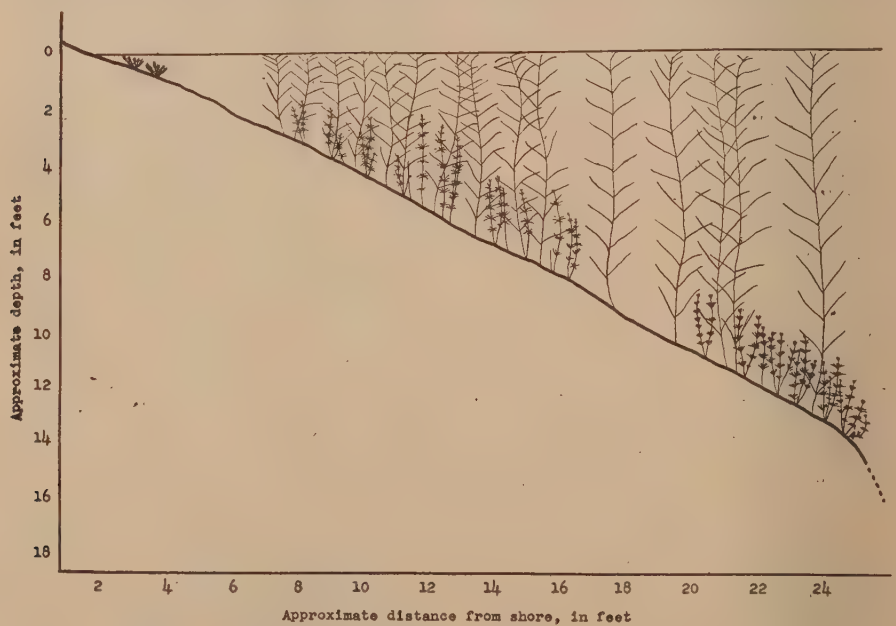

FIG. 2. Vertical zonation of aquatic plants in Salt Pond, Falmouth, Mass., July, 1947, with special reference to Characeae. Major constituents: 0–1 ft., *Chara delicatula* (tufted form) and *C. canescens;* 1–3 ft., bare pebble-sand; 3–8 ft., *C. delicatula* (elongate form) and *Potamogeton* sp.; 8–10 ft., *Potamogeton* sp.; 10–13 ft., *C. Braunii* and *Potamogeton* sp.; 13–? ft., not known.

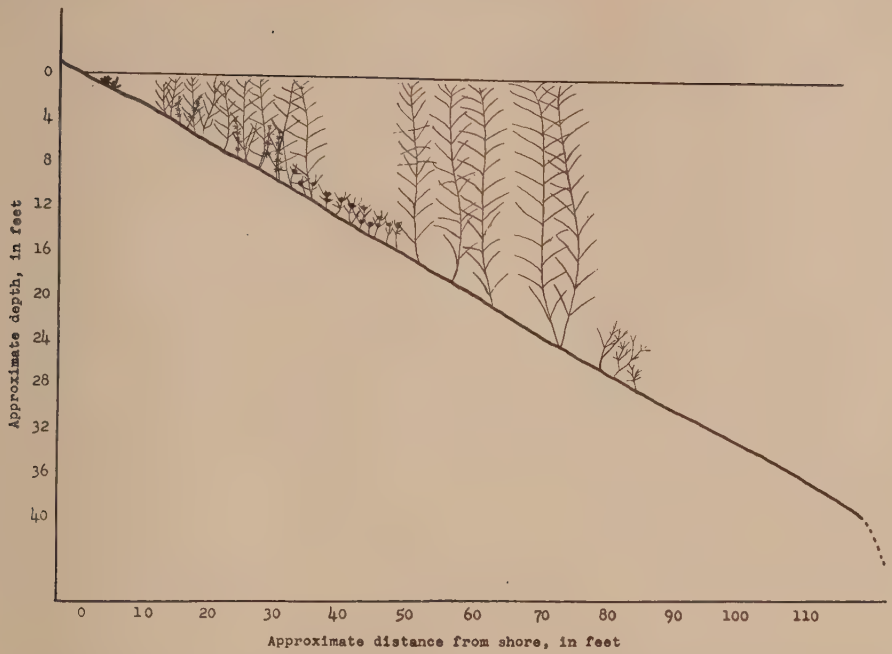

FIG. 3. Vertical zonation of aquatic plants in Keuka Lake, Keuka, New York, August, 1946, with special reference to Characeae. Major constituents: 0–2 ft., *Chara contraria* (tufted form); 2–5 ft., bare sand; 5–15 ft., *C. contraria* (elongate form) and *Potamogeton* sp.; 15–20 ft., *Tolypella fimbriata;* 20–30 ft., *Potamogeton* sp.; 30–40 ft., *Nitella flexilis* (sterile); 40–? ft., no vegetation found.

interpretation has been assembled from the writer's study of herbarium specimens. The data (table II) indicate that certain species have occurred in given habitats during periods exceeding fifty years, and that during these years collections have occasionally been made. The data do not prove that the species occurred continuously during the period, but they do indicate that conditions in these habitats were such as to either consistently support a vegetation dominated by certain species of Characeae or to repeatedly re-establish one represented by the same species. Thus, one can hardly consider Characeae as being transitory under all circumstances; rather, they may form a relatively stable vegetation in certain habitats. If these plants form a vegetation that is relatively stable under certain environmental conditions, they may be considered a significant ecological constituent of the vegetation.

ZONATION OF CHARACEAE

If one accepts the inference that the Characeae may be considered a significant portion of the vegetation once it has become established in a relatively stable environment, the question arises whether the species exhibit any important ecological differences. In seeking an answer to this question, vertical zonation was selected as one aspect relatively simple to attack. The method employed was to run line transects, perpendicular to the shoreline, along the bottom into deep water, and to record the zonation of plants represented. Observations were made by wading in shallow water, subsurface swimming and observing the vegetation through a face mask, diving with a diving mask in deeper water, and dredging with a plant hook in depths in excess of the limits of the other methods. Dredging was found to be the least reliable of the methods, and was used only when necessary. Subsurface swimming was considered the best. The depths of water and distances from shore were estimated. The results of these studies are expanded below.

At Weeks Pond, Falmouth, Massachusetts (fig. 1), the zonation exhibited an emergent zone of scattered *Gratiola lutea* Raf. and a floating attached zone of *Nymphaea odorata* Ait. Below this, from a depth of three to five or six feet, was a wide bed of *Nitella transilis* T. F. Allen. Beyond this depth occurred a shelf which dropped to about nine feet. At the edge

of this shelf, Potamogeton formed a distinct zone. As the bottom leveled off, the Nitella again carpeted the bottom on into deeper water. Here, then, "Chara" occurred both inside and outside the zone of attached submerged aquatics.

Salt Pond, Falmouth, Massachusetts (fig. 2), had a basin with a steady slope downward as far as the writer could effectively penetrate by surface diving (approximately fourteen feet). Most of this slope was vegetated by a broad zone of Potamogeton. However, inside this zone the shallow water was vegetated by *Chara delicatula* with an occasional *C. canescens* Desv. ap. Lois. From about three to eight feet, the Potamogeton zone was found to be a mixed population of Potamogeton and an elongated form of *C. delicatula*. From about ten to twelve feet, the Potamogeton was mixed with a different species, *C. Braunii*, which extended some two or three feet beyond the Potamogeton zone. In this case, the "Chara" occurred in the innermost zone, throughout the attached submerged aquatic plant zone, and outside of this zone in deep water.

At Lake Keuka, New York (fig. 3), just off Keuka, the slope of the basin is more or less constant to a depth of approximately forty feet. The vertical zonation here showed a spotty zone of tufted *C. contraria* Braun ex Kütz. to a depth of about two feet. From five to eight feet, a zone of Potamogeton was found to be a mixed population with elongate specimens of *C. contraria*. At a depth varying from six to fifteen feet on down to twenty feet, the Potamogeton vegetation was broken by openings. In these openings were found solid mats of Tolypella, largely *T. fimbriata* T. F. Allen. Below these openings, the Potamogeton extended from about twenty to twenty-five or thirty feet with no "Chara." Below this depth the Potamogeton disappeared, and *Nitella flexilis* (L.) Ag., another Charad, extended to a depth of thirty-five to forty feet. No vegetation was recovered at a depth greater than forty feet. Here, then, the various species of Characeae were sorted into distinct zones consisting of distinctly different species (and genera).

Discussion

On comparing these data with the usual concept (fig. 4) of vertical zonation in lakes, one notices a distinct difference. The usual concept seems to indicate zonation including emergent plants, floating submerged plants, sub-

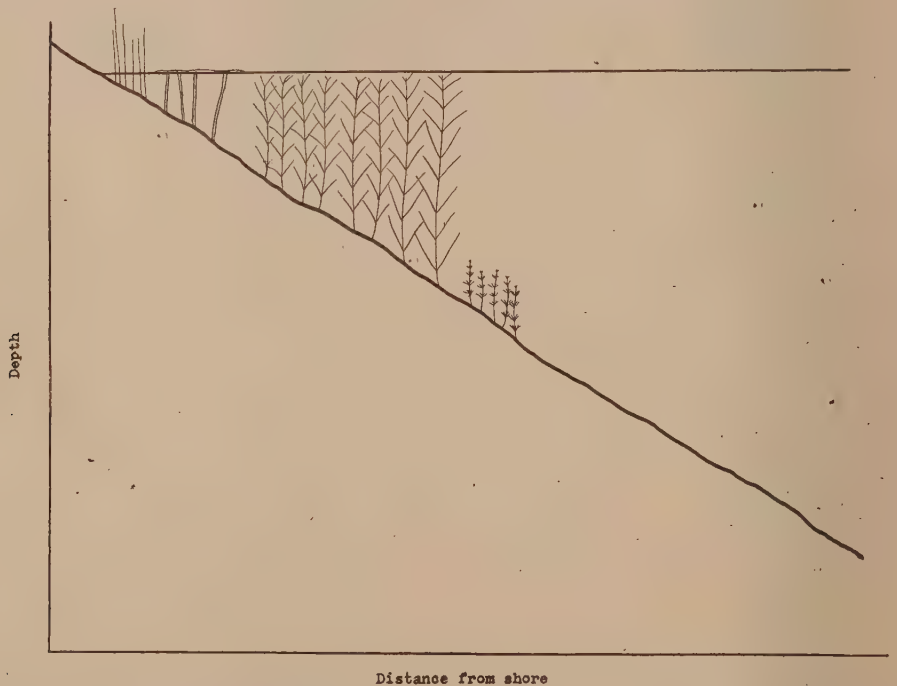

Fig. 4. The usual concept of vertical zonation of aquatic plants. The zonations include the emergent, floating attached, submerged attached, and finally the Characeae.

merged attached plants, and finally the Characeae. Our data indicate that the Characeae are not restricted to the outermost zone. In fact, they may occur above, among, and below the submerged aquatics. Furthermore, they may form distinct zones consisting of different species (and/or genera) of Characeae. Thus, the fact that such zones exist indicates that the various species do exhibit significant ecological differences.

In studying the aquatic vegetation in a body of water in which Characeae occur, it should therefore be of some interest and importance to consider the species and genera involved, and not just lump the entire group under "Muskgrass" or "Chara" as is a popular practice in this country.

Summary

1. A study of a small pond and herbarium specimens collected from several lakes indicates that Characeae may be transitory plants or may occur for fifty or more years in a given habitat.

2. Transects made in the vegetated zones of three lakes indicate that the Characeae are not restricted to the outermost zone as is a common concept. They may occur above, amid, and below the zone of attached aquatics.

3. The Characeae frequently sort out into zones represented by different species (and/or genera), thus indicating differences in the ecology of the various species.

4. It is concluded that studies of aquatic plant ecology should take cognizance of the different species of Characeae wherever feasible rather than lumping them as "Muskgrass" or "Chara."

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THE VERTICAL ZONATION OF *ACMAEA*, THE LIMPET

Introduction

The vertical zonation of organisms in the intertidal area is a result of variation of the environmental conditions due to the periodical rise and fall of the tide. These conditions are salinity, temperature, wave action and exposure to air. How tidal action determines definite zonal limits is of basic interest. Doty ('46) found a large number of marine algae to be limited vertically by what he termed critical tide factor levels, i.e., discontinuities in curves of exposure and submergence time introduced by various components of the tides. Organisms must be adapted to resist extremes of environmental conditions in order to exist at various levels in the intertidal area. Orton ('32) believed that an adaptive difference of form accounted for the ability of limpets of the genus *Patella* to resist desiccation. According to Orton, the limpets at higher levels are relatively taller and thus can store more water between tides, but Shotwell found in limpets of the genus *Acmaea* that variations in shell shape are not correlated with position in the tide zone but instead are a result of growth. Smaller limpets of this genus can exist high in the intertidal area by virtue of a relatively greater storage space for water in the subnuchal cavity between the shell and mantle, whereas large ones are restricted to the lower limits of the species' range. Orton's published data show small limpets to be high in the intertidal while large ones are lower. It seems likely from this that *Patella* is distributed much the same as *Acmaea*, that is, on the basis of size, not shape.

The purpose of the present study is to determine the limits of vertical distribution of the limpets of the genus *Acmaea*. The factors that define these limits are discussed.

Appreciation is expressed here to F. A. Gilfillan, Director of the Oregon Institute of Marine Biology at Charleston, Oregon, for making available facilities during the period of this study.

Methods

Over five hundred limpets of the genus *Acmaea* were collected from various intertidal levels in and around Sunset Bay, Oregon, a small coastal bay just south of Coos Bay. Species represented were *Acmaea digitalis, A. mitra, A. scutum, A. testudinalis scutum,* and *A. pelta.* These specimens were used in an earlier study (Shotwell, '50).

Discussion of Results

The vertical distribution of the species of *Acmaea* considered is shown in Figure 1. Also included are the critical tide levels which coincide with the limits of the species distribution.

To determine why zonation occurs as it does, it is necessary to examine the form of the tide

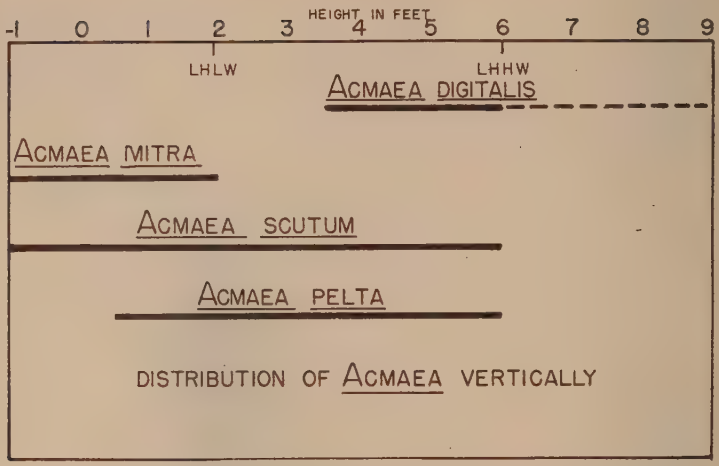

FIG. 1. Distribution of *Acmaea* in the intertidal zone at Sunset Bay, with position of important critical tide levels included.

curve. On the Pacific Coast of North America the two high tides as well as the two low tides each day are of different heights. For this reason it is necessary to speak of higher high water and lower high water, higher low water and lower low water (see fig. 2). Because of this difference an organism living just above mean lower high water will suffer exposure to air for twice as long a time, on the average, as one living just below that level. But this is by no means the whole story, as Doty has shown. Intertidal organisms are not subject to average tides, but to constantly changing tides. The semi-diurnal variation is responsible for only some of the sharp discontinuities that may be supposed to operate as critical limits. Near summer solstice all the tides, high tides as well as low tides, are lower while the tides are higher near winter solstice. An organism just above the level of lowest higher high water is submerged for a few minutes each lunar day most of the year; at the time of summer solstice, however, the highest tide of the day just fails to reach it, and before the second day has brought a higher tide the organism is killed by exposure.

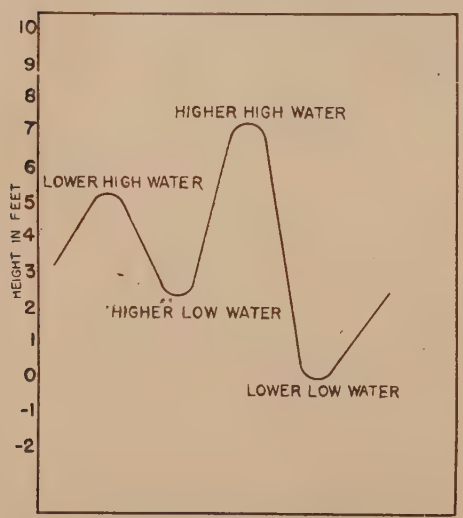

FIG. 2. Maregram of a typical day's tide on Pacific Coast.

Each of the extreme high or low levels of the year may be similarly thought of as a critical level for the long-continued existence of some organism. It is particularly to be noted that the lowest levels are reached in the summer, when the effects of exposure to air are increased by high-angle insolation and clear skies. The critical tide levels are shown in Figure 3, the derivation of which is fully discussed by Doty.

It may be seen from Figure 1 that the upper limit of *Acmaea mitra* is in close agreement with the level of lowest higher low water. The upper limits of *Acmaea scutum* and *Acmaea pelta* coincide with lowest higher high water, while *Acmaea digitalis* occurs sparsely if at all above that level. The area above lowest higher high water is inhabited by very small limpets of the genus *Acmaea,* some of which are *digitalis.*

The lower limits of ranges cannot be explained by desiccation but are probably a result of competition for space and food.

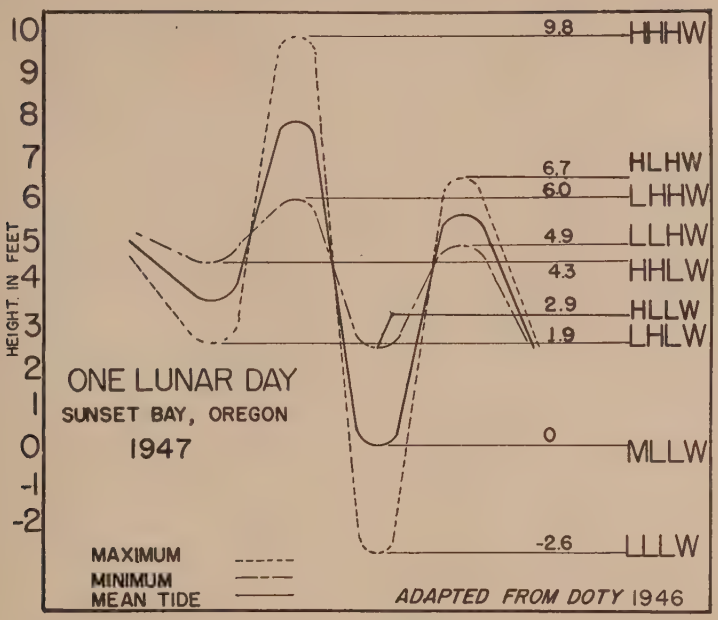

FIG. 3. Critical tide levels as predicted by tide tables in Sunset Bay. These are shown as the maximum and minimum tides, HHHW (highest higher high water), HLHW (highest lower high water), LHHW (lowest higher high water), LLHW (lowest lower high water), HHLW (highest higher low water), HLLW (highest lower low water), LHLW (lowest higher low water), MLLW (mean lower low water), and LLLW (lowest lower low water).

Test ('45) attempted to show the vertical distribution of *Acmaea* to be dependent upon the vertical ranges of specific algae used by each species as food. Since it is shown here that the vertical ranges of *Acmaea* species coincide with two critical tide levels, and since Doty shows many marine algae to be limited at the same levels, it seems equally possible that instead of *Acmaea* being limited by its food, the food and the limpets are limited by the same factors. Desiccation may well be the primary factor in the distribution of *Acmaea*.

Conclusions

The upper limits of the intertidal ranges of species of *Acmaea* at Sunset Bay, Oregon, are in agreement with certain critical tide levels responsible for extremes of desiccation.

Two species are sharply limited at the level of lowest higher high water, a third is very sparsely distributed above that level, while a fourth drops out at lowest higher low water. It is suggested that if the vertical distribution of limpets is governed by the occurrence of particular species of algae used as food, this is because the algae and the limpets are both limited by the same physical factor, namely, the maximum time of uninterrupted exposure to air during the course of a year.

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ECOLOGICAL NOTES ON THE UPPER AMAZON

A hurried trip down the Río Ucayali and the Río Amazonas in eastern Peru and Brazil gave opportunity for certain observations on the general ecology of the banks of these rivers which seem worth putting on record. Time was not available for careful investigation of any of the phenomena noted, and often it was not possible even to secure specimens of the plants and animals concerned, especially as some of the observations were made from the decks of river boats. Fortunately the courses of these boats run generally close to one bank or the other, so that observation is not impossible. Fortunately, too, certain of the important plants concerned belong to genera whose identity is obvious even from a distance.

The Río Ucayali is one of the three great rivers which unite in eastern Peru a few degrees south of the equator to form the greatest of all rivers, the Amazon. The others are the Río Huallaga and the Río Marañon. They are joined shortly below Iquitos by the broad Río Napo. Some distance below this, at intervals, enter the Río Putumayo, the Río Caquetá, the Río Purus, and the Río Negro, at Manaos. The present observations were made between a point about 30 km above Pucallpa on the Río Ucayali and Manaos, at the mouth of the Río Negro. Stops of some duration were made at Pucallpa, Iquitos, and Pebas, but because of uncertainty of transportation schedules these could not be utilized to full advantage. Short or momentary stops were made at many other localities.

These rivers, especially above Pebas, are characterized by meandering courses through broad silt plains, with the resultant cutting off of meanders to form C-shaped lakes or "cochas," and with conspicuous cutting away of land on the concave sides of the curves and building up of bars on the convex sides. In the upper portions of the Ucayali the general level of the plain is well above the ordinary levels of the water, and only very high water causes consequential floods, except on recently formed land. This level becomes lower in the lower Ucayali and Amazon, and ordinary high water, such as happens for a large part of each year, results in extensive inundation of the land near the river except for localized areas locally called *"restingas"* which are 10–15 m above the level of the surrounding plain. These are well exemplified by the area on which Iquitos is situated. They are scattered at intervals along the river, from the village of Orellana, on the Ucayali, on down. They may be several kilometers in extent, and their drainage is usually away from the river either into smaller rivers running parallel to the main river for a distance or into small streams which cut through into the river. On the Amazon the distribution of restingas is curious. Above Leticia they are mostly on the north side of the river. At Leticia they are on opposite sides, at Leticia and Ramon Castillo. Below this they are to be seen practically only on the south bank. From some distance above the mouth of the Río Purus and thence down the river no restingas were seen though there are local areas slightly above the general level of the flood plain. I have heard no convincing explanation of their existence. Though both *"restinga"* and *"varzea,"* or flood plain, are covered by dense tropical rain forest, the floras of the two habitats are quite distinct. It was not possible to make complete observations on the floral composition of any area on this trip.

A sharp distinction is to be noticed between the soils along the Río Ucayali and the Amazon. The characteristic soil along the Ucayali flood plain from Pucallpa on down is a fine yellowish silt. On entrance into the Amazon an immediate change is noted. The plain is now made up of a gray sand, very fine, but definitely a sand. This apparently reflects the fact that the basin of the Río Marañon lies in a sandstone area. This sandy nature is evident for some distance down the Amazon. By the time the mouth of the Río Caquetá is reached it has changed to a gray clay. The soil of the restingas is red or yellowish clay varying in places to sand, sometimes a pure white sand. There are strata of gravel in some of the restingas at Pebas, that are exposed by erosion, where the sand or clay is filled with quartz pebbles. In general, these Amazonian soils, as with most tropical soils, are notably sterile. The "A_1 horizon" is infinitesimally thin or absent. Kicking aside the duff or dried leaf layer, one exposes clay or sand. "Chacras" or patches cleared for agriculture are abandoned after a short time. On the restingas this is about two or three years. On the flood plains the annual silt deposit renews, to a certain extent, the fertility, but the extent of abandoned clearings now in second growth or *"purma"* shows that even this rejuvenation is not sufficient compensation for the rapid and complete decomposition of organic matter that characterized the soils of warm countries.

The ragged appearance and uneven ages of the trees, and the dense undergrowth and second story, in much of the forest visible from the river are good indicators of the history of the region. Though the human population is small, the agricultural method followed of clearing, planting for a few years, then allowing the jungle to return, gives this character to great stretches. An undisturbed rain forest presents an aspect of a dense growth of trees of more or less even height, typical umbrella shape, with

clean trunks, little undergrowth, and a dense canopy of vines in the treetops. The practice of clearing, leaving standing the really large trees that are difficult to fell, gives the uneven appearance to be seen in so much of the riparian jungle along the Ucayali and Amazon. Logging out of the great trees of *"cedro"* (*Cedrella* sp.) and mahogany also contributes to this aspect. This is true, especially, of much of the restinga. Because of the fact that these latter areas are not flooded, they present attractive sites for settlements. Almost all of the villages along the upper Amazon are on restinga land. Agriculturally, however, such places are practically worthless. But, as is typical of human practice, they have almost all been tried out. The cutting of wood for the numerous wood-burning steamers of the Amazon system is another factor in the decadence of the riparian forests. Great quantities of wood, especially "capirona" (*Calycophyllum*) and other hardwoods, are used to provide motive power for the river traffic. The result of all this human activity is that the greater part of the jungle to be seen from the river is *"purma"* or second growth.

Virgin forest may be identified by the predominance of large old trees of more or less uniform size, but of many kinds with a continuous canopy of their umbrella-shaped tops, filled with lianas. The aspect presented to the river is one of a solid wall of green, but once this mass of vines and brush induced by the sunlight is penetrated, there is relatively little undergrowth and one may wander more or less freely among the huge columnar trunks in this dim, twilit floor of the lowland tropical rain forest. *"Purma"* or second growth presents a mass of vines and brush or, in places, scitaminaceous plants on the forest floor that is well-nigh impenetrable. The factor of the entrance of sunlight to the forest floor makes all the difference in the world.

The outstanding ecological phenomenon to be observed along the upper Amazon is the vegetational succession on the built-up lands on the convex sides of the meanders. On the concave sides, opposite, where the river is cutting away the land, the primary forest or, in case the land has been occupied, the purma, is exposed in section and may be seen to best advantage. Where bars or *"playas"* are being deposited and built up a striking succession is evident. Its stages are sharp and clear-cut.

Recently exposed land is completely occupied by *"gramalote,"* [1] a coarse grass or reed association which seems to be the characteristic riverbank vegetation everywhere in this region. The width of this belt varies with the width of fresh deposits. In form it is a dense, tangled low cane-brake, here and there mixed with, or even replaced by, stands of young plants of *"pajaro bobo"* (*Tessaria integrifolia*), a common wet-land plant throughout the northern and central parts of Andean South America. This reed belt is always flooded at even reasonably high water. Patches of it are characteristically torn loose by floods and carried down the river.

Back of this, and sharply set off from it, is a belt of tall brakes of the enormous reed *"caña brava"* (*Gynerium sagittatum*), mixed with *"sause"* or willow (*Salix chilensis*) and grown plants of *Tessaria.* The latter does not naturally form a large tree, and the willow here never seems to have a chance to, because of the immediate succession of the next stage.

This is a distinct belt of a solid stand of *"setico"* (*Cecropia* sp.) which crowds out all but part of the *"caña brava."* The *Cecropia,* a weird-looking tree of the *Moraceae* with great palmately lobed peltate leaves and candalabra-like branches inhabited by colonies of red ants, forms almost pure stands, forests 10–15 m tall. These are a characteristic feature of the landscape of the upper Amazon system.

After a time *"ojé"* (*Ficus* sp.) and other aggressive trees of the primary forest gain a foothold and the setico forest becomes mixed. Later the *Cecropia,* essentially a pioneer tree in these situations, gives way to the tall mixed tropical rain-forest that is the basic primary or "climax" vegetation of the wet lowland tropics.

This succession seems to be best developed along the Río Ucayali and on the Amazon to some distance below Iquitos. After the Brazilian border is passed it tends to become less clear. The *caña brava* belt, especially, becomes less well marked and finally drops out altogether, except for occasional strips or patches of willows and *Tessaria. Gynerium* itself was not seen at all below Codajas, and there only doubtfully, at a distance. The *Cecropia* belt does not disappear, but becomes less well marked, occuring more as irregular patches, and mixed with other pioneer trees. It usually seems to follow directly after the reed belt, which continues to be well marked.

The reason for this striking change is not altogether apparent, but it is more or less correlated with three factors. These are the increase in size of the river, the increase in radius of its meanders, and finally the apparent

[1] *"Gramalote"* along the Amazon system is a mixture of coarse grasses of similar habit composed, according to J. R. Swallen, of one or more of the following species, which may be present in different proportions in different places: *Echinochloa spectabilis, Paspalum repens, Hymenachne donacifolia, Paspalum fasciculatum, Hymenachne amplexicaulis, Oryza perennis, Oryza grandiglumis,* and *Panicum elephantipes.*

predominance of cutting-away of land over building of exposed bars and flats. There are certainly fewer areas upon which a succession may take place, and the process, as it exists, is more often seen on steeper banks rather than on extensive flats.

In a young stand of *Cecropia* on the Río Ucayali below Contamana an opportunity was afforded to observe the process of colonization by the red ant (*Podomyrma* sp.) that is the universal inhabitant of the cavities in the internodes of this tree. The seedling Cecropias were from 8 to 14 dm tall, as yet unbranched. Those over 1 m tall had developed hollow internodes. On some of these larger plants holes were noticed just below each node. On others queen ants were seen busily chewing similar holes into the soft stems. Inside each internode where the holes had been completed was found an ant. In several cases rainwater had accumulated in the cavity and drowned the ant. The ants digging the holes or already inside had either just lost their wings, or the wings broke off very readily. Older trees nearby were cut down and examined. With the exception of a few wandering individual ants on the outside of the trunk, the ants were in the young growing parts of the branches. At any disturbance they emerged in swarms, running rapidly and apparently aimlessly around over the surface of the branches, ready to punish and effectively repel the intruder.

The floating vegetation on the Amazon at this season, though obvious, is not very varied. The most abundant plant is the water lettuce (*Pistia stratiotes*). It is accompanied by the water hyacinth (*Eichornea crassipes*). These two plants, along with one or two other much rarer ones, form what might be termed the natural component of the floating vegetation. They abound in the eddies and quiet water close to shore, tangled with the reeds and riverbank vegetation, and at high water numerous individuals are swept into the current and go floating down the river.

The other component, perhaps to be termed the extraneous component, is composed of floating masses of the gramalote, or reed, torn loose by the flood waters and carried along down the stream. These masses are sometimes a number of meters across and present the appearance of natural patches of vegetation in good condition in spite of their situation. It is undoubtedly these which have given rise to the tales of "floating islands" so current in narratives of Amazonian travel, and which have figured so strongly in certain ill-founded attempts to explain the distribution of species and floras.

There seems to be practically no foundation for the idea that these masses of grass have any role whatever in the distribution of any species except those of which they are composed. Observation of many of them being run down by river boats fails to yield the slightest indication that there is any soil carried along by them. Only once was any other living vegetation seen tangled with one of these "islands." Their origin seems to be well up in the system, and lower down, near the mouth of the Río Negro, most of them were seen to have become waterlogged and to have collapsed down to water level, with death of the reeds progressing rapidly.

One or two tree trunks were seen floating with living plants growing on them. Also, above Pucallpa was noticed an accumulation of floating driftwood in an eddy with grass growing on it.

During the trip one very curious and apparently rare phenomenon occurred. In Iquitos after the 12th of November reports began to appear in the local newspapers of great quantities of debris, including quantities of tree trunks, enormous numbers of dead fish, dead animals, and even human bodies, floating past Pucallpa and Contamana. Warnings were issued by Peruvian government agencies against drinking the polluted river water. References were made to a probable origin of this condition in a severe earthquake which took place on November 1 with its center in the Cordillera not far from the upper reaches of the Río Ucayali.

No particular attention was paid by me to these reports until November 20th when I travelled in a small boat which drifted from the mouth of the Río Napo to near Pebas, a few miles below. During the whole of the trip the surface of the Amazon, especially where the current was strongest, was covered with driftwood and vegetable debris with which were thousands upon thousands of dead fish of all sizes up to almost two meters in length, and in varying stages of decomposition. One or two mammals were noticed, but these were decomposed beyond recognition. Most of the fish seemed to be of the catfish group, though there were many other kinds. The freshness of many of them suggested that they could scarcely have been part of what reportedly passed Pucallpa a week or two earlier. The stench was indescribable. A current and apparently acceptable belief along the river was that many of these fishes had died from eating the decomposed fish and animals floating down from above.

The duration of the height of this pollution as it passed Pebas was about five days. An important feature was that practically all of the floating wood was typical driftwood, waterworn and well rotted. It looked as though it were compounded of the accumulations caught in eddies and cast up on shores up the river which

had been picked up and carried away by a sudden rise in the river.

Various wild theories were propounded locally of landslides caused by the earthquake either filling the river with debris and suffocating the fish, or blocking up the river, then suddenly giving way with a rush that killed everything in its path. The condition of the driftwood and the lack of any unusual number of fresh trees would tend to discount any of these theories even had they appeared capable of explaining the disaster. The only two actual unusual circumstances external to the occurrence itself were the earthquake of November 1 and unusually high water for the month of November. I have no suggestion of an explanation.

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REMARKS ON THE FACTUAL BASIS OF ECOLOGY

Some time ago I happened to see one of the country's leading ecologists pull a scrap of a plant from his pocket and ask a taxonomist what it was. He wrote down the name given him by the taxonomist, then threw the scrap away. This seemed curious, but I thought little of it until, some time later, I saw another prominent ecologist do precisely the same thing. Then I began to think about the methods of work in ecology.

One of the impressive things about much ecological investigation is the meticulous accuracy with which quadrats are laid out and counted, instruments read, chemical analyses made, and with which data are handled statistically. Insofar as biological data can be effectively expressed quantitatively and statistically, it surely seems that the principles emerging from these studies are likely to be sound.

The specific data gathered and used by ecologists consist, in a large measure, of two kinds—the quantitative information just mentioned, and the identities of the organisms studied or constituting the communities studied. In view of the incidents mentioned above, and of many others that indicated a rather casual attitude toward careful determination of plants among ecologists, I was prompted to examine recent ecological literature to see if evidence of this carelessness actually appears in print.

It has always appeared axiomatic to me that scientific data, to be of real value, must be verifiable. This does not present a serious problem in the physical sciences, as the phenomena dealt with are of a permanent or recurrent nature, or are such as can be repeated at will. In the social sciences this is usually an insoluble problem, and therefore a truly scientific approach is impossible to most aspects of the social sciences. Biology is more or less intermediate in this respect. Ecology is, perhaps, the most refractory branch of biology in the verifiability of its data, since it deals with extremely dynamic phenomena. In its environmental aspects, unreliability is avoided, in a measure, by making great numbers of observations and testing the value of the data statistically. The determinations of the organisms dealt with can only be considered reliable if they are verifiable, that is, if the material has been preserved in such a fashion that any subsequent worker can re-examine it and check the identifications.

To get an indication of actual practice among American ecologists, all articles dealing in any way with plants in volumes 25–30 of Ecology and in volume 14–18 of Ecological Monographs were examined carefully. Since these are the official journals of the Ecological Society of America this may be a fairly representative sample of current practice. Five categories were set up as follows: (1) No specimens cited or mentioned at all. (2) Some specimens mentioned, but not for all species named, no record of the herbarium in which they were deposited. (3) Same but with place of deposit recorded. (4) Specimens cited for all species mentioned, but no record of place of deposit. (5) Same but with place of deposit recorded. All articles using plant binomials were scored. For the six volumes of Ecology, but not for the Ecological Monographs articles, the number of binomials used was counted.

The results of this tabulation were eloquent. Two hundred and ten papers were examined. In 170 of them there was no mention of specimens. In 26 a few specimens of doubtful species were mentioned as having been collected, but no mention was made of where these specimens could be re-examined. In 4 papers some specimens of doubtful species were mentioned and place of deposit noted. In 4 more, specimens were cited of all species, but no mention made that they had been deposited in a permanent collection, or even that they were kept. In 5 articles out of the 270, collections were cited of all species and it was stated that they were deposited in specified institutions.

Of the 3,480 binomials mentioned in the 164 articles examined in the six volumes of Ecology, 2,970 are thus completely unsupported by anything—as far as the evidence is recorded these are just the guesses of the authors. Two hundred and sixty-seven are possibly based on

actual material, but there is no way of knowing where this is, should it be desirable to verify the identities. Two hundred and forty-three rest on specimens available for examination at a designated herbarium.

I very seriously doubt that many ecologists have ever stopped to consider how this apparently general disregard of the importance of accurate identification of their plants lessens the value of their work. Some of them may even have blissful confidence that their identifications are right, either because they think they know their plants, or because they have taken scraps to a taxonomist for determination. They forget, or do not know, that the taxonomists have so much of a realization of their own fallibility in this matter that they almost always cite the collections that they have examined in preparing a piece of work, with the institutions in which they are deposited.

That some of these ecological authors have little conception of what is involved here is evident from such footnotes as, "The authority for the scientific names is Tidestrom's Flora of Utah and Nevada," or "All nomenclature of grasses is based on Standardized Plant Names ('42)." That a book can, in itself, be an authority for names used is naïve. And that nomenclature can be based on a mere list such as Standardized Plant Names is apparently making the common name the basis for the application of the scientific name. Actually it would be really far better to use only common names, and thus admit the actual uncertainty that exists in the data, rather than translating them into Latin names to create a false sense of reliability.

Awareness of the importance of determinations that can be checked is not completely absent among ecologists, as is shown by a remark of Lawrence, Lawrence and Seim (Ecology 28: 77, 1947) recommending the preservation of herbarium material of parent plants as one of the "highly important desiderata in making reports on seed germination of native plants." It would seem to me important in all work of any kind that deals with plants. Herbarium labels on specimens collected by Frank E. Egler bearing the statement "collected to authenticate Vegetation Studies" may also be cited.

It is truly unfortunate that followers of other branches of botany have allowed the old resentment against the former dominance of systematics in botany and their annoyance against the name changing that has resulted from honest difference of opinion and from correction of the errors of the past to impair the quality of their own work. I will take the liberty to quote from a recent letter from Edgar Anderson, "Outside the field of pure taxonomy, I think there are a number of biological disciplines which might well adapt the herbarium idea to their own uses. The stamp collector tradition in taxonomy has had such a cramping effect on the development of real accuracy and maximum usefulness of herbarium specimens that non-taxonomists, repelled by this old-fogyism, have yet to learn what a powerful technique it really is. . . . I think that modified herbarium technique would be of wide usefulness in physiology, genetics, plant breeding and ecology." This was a comment that did not come in answer to a question of mine, but only in the course of discussion of another article.

There is no question that the preparation of specimens would add to the work involved in an investigation and there are certainly situations in which it is impossible, such as the famous train-window botany, or, to cite a case where I, myself, am guilty, observations from a river steamer, or airplane. But, considering the amount of labor that goes into sampling by quadrat methods, physiological investigations in autecology, or digging root systems, the addition would not be out of proportion, in view of the additional accuracy achieved. And as for citing specimens after they are collected, it would add from a line to a page or two to the length of most papers. It seems a pity to do an extensive piece of work on a single species, for example, and take a chance of undetectable error to save the trouble of drying and labeling a single plant and adding a line to a report.

It is highly likely, furthermore, that some of the differences of opinion that often arise in ecology might disappear if it were ascertainable that actually different species or varieties were under observation by the parties to a dispute. Certainly some of the unlikely points in Pacific Islands vegetation study have been cleared up by the receipt of material collected there by some of the Japanese workers.

It is true that curators of herbaria are not always enthusiastic about preserving material sent in by ecologists. Sometimes it may very well not be worth preserving. However, if the same care were given to the preparation of specimens and the provision of adequate data as goes into digging a root system, this indifference would doubtless soon disappear. Many curators would immediately recognize the much greater importance of good specimens supporting ecological observations, compared with the average run of material collected by pure systematists or casual collectors.

Certainly many ecological reports will rest on a firmer factual basis if a permanent record, in the form of specimens on deposit, is available for future reference and re-examination.

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A NEW LOCALITY RECORD FOR *BRANCHINECTA COLORADENSIS*, WITH HABITAT NOTES ON TWO SPECIES OF FAIRY SHRIMP IN CENTRAL TEXAS

Branchinecta coloradensis is generally regarded as an alpine species, the original description of Packard ('74) being based on material from a Colorado mountain pool south of Leadville at an altitude of 12,500 feet. Other Colorado collections from permanent ponds and mountain pools at 11,000 to 12,000 feet elevation have been reported by Packard ('83), Ward ('04), Shantz ('05), and Behre ('31). Creaser ('31) noted that the species had been collected from "a hollow in a boulder," near Estes Park, at 8,000 feet elevation; and collections from small hollows in granite outcroppings near Fort Collins and Estes Park at 6,800 to 8,000 feet elevation were reported by Gordon ('32). Gordon noted that the animals were frequently quite abundant in these little hollows, but were smaller in size than individuals from alpine ponds, a situation which he suggested might be due to the limited food supply of the temporary puddles.

During the summers of 1948 and 1949, the writer made collections of *B. coloradensis* from temporary pools in Llano County, Texas. This appears to be the first record of the species from the state. The habitat of the animals was unusual and appears worthy of fuller description.

The so-called "Central Mineral Region" of Texas is an area of igneous intrusions, mostly granites, through the overlying Paleozoic and Mesozoic sedimentary beds. The Region includes all of Llano, and parts of the surrounding counties. One great granite dome, situated on the county line between Llano and Gillespie Counties, is known locally as "Enchanted Rock." It is several hundred acres in area and rises steeply 500–600 feet above the surrounding countryside. The elevation of the summit is approximately 1,815 feet. There are no permanent bodies of water on the "Rock" but there are numerous small, shallow rock basins which may contain a few inches of water after heavy rains. These rock basin pools are all quite unshaded; they are floored with granite pebbles and sometimes a film of windblown soil.

From one of several such pools containing fairy shrimp, a small collection was made on July 17, 1948. The pool was about twelve feet in circumference and had a maximum depth of only three inches (fig. 1). The water was very clear; the pool was quite devoid of vegetation. No facilities were available for determining physico-chemical factors other than hydrogen ion concentration which was pH 6.6. The phyllopods collected were small but mature specimens of *B. coloradensis*. Males averaged 10 mm. in length; females, which all bore well-filled egg sacs, averaged about 9 mm. Very small chironomid larvae, small mayfly naiads, nematodes, ostracods, and numerous conchostracans (*Leptestheria complexmanus*) were collected from the same pool.

These pools all dried up within the next few days and were not observed to contain water again during the remainder of the summer. Observations were terminated at the end of August, 1948.

The locality was revisited several times during the summer of 1949. On June 14, the rock basins were well-filled and, from a grass-bordered pool close to the one previously described, a collection of approximately 260 *B. coloradensis* was made. The animals were small, both sexes averaging only 7 mm. in length. The ovisacs of the females usually contained only two or three small eggs, although one 9 mm. individual was taken carrying 12 eggs.

On June 28, 1949, and, subsequently, on July 12 all pools were observed to be completely dried up.

During the five day period, August 5–9, unusually heavy and widespread precipitation occurred in the region. The nearest United States Weather Station, at Doss, about ten miles to the southwest, recorded 2.17 inches of rain during this period. When "Enchanted Rock" was again visited on August 16, 1949, the pool contained about three inches of water and harbored a rather scanty population of *B. coloradensis*. This is the first instance known to the writer of the species appearing twice in the same pool during a single summer although, in view of the small size of the individuals of the first brood, it is possible that this August brood simply represents a second hatching from eggs deposited the previous season. The size of the animals was rather larger than that of the brood noted earlier; males averaged 10 mm. in length; females 9.5 mm. At 9:00 A.M., with the air temperature (shade) at 29.2° C., the water temperature was observed to be 27.8° C.; doubtless it was several degrees higher than this at mid-day. In this connection Shantz ('05) reported that *B. coloradensis* disappeared from waters of Dead Lake, Colorado, in August when the surface temperatures reached 15.6° C. He noted, however, that a contributory cause of the death of the animals in this case may have been the growth of a green algae, *Characium*, which covered the legs and caudal appendages of the shrimp to such an extent that they could hardly swim.

Packard ('83) reported the occurrence of

FIG. 1. Rock basin pool on summit of Enchanted Rock, Llano County, Texas. The habitat of *Branchinecta coloradensis.*

Streptocephalus scalii Ryder twice in the same pool near Woodbury, New Jersey during a single summer season. This observation has been cited by Pearse ('18) and Creaser ('30). Dexter ('46) and Dexter and Kuehnle ('48) reported double broods of *Eubranchipus vernalis* (Verrill) in temporary pools in northeastern Ohio, but attributed the phenomenon to a second hatching from an earlier deposition of eggs. As far as the writer can determine, two generations during a single summer in a pool which dried up in the interval between has not been reported for *Streptocephalus texanus* Packard. Observations on the latter species which may be subject to this interpretation are given below.

Two small temporary pools were observed early in the summer of 1949 about four miles south of Doss in Gillespie County, Texas. These pools were located in a dry stream bed, a small tributary of Threadgill Creek. They were shallow, hot, and muddy; about thirty feet long, six to eight feet wide, and less than twelve inches deep. One pool was shaded at its lower end; the other was entirely exposed. Both were extremely turbid due to suspended silt and a heavy growth of plankton algae.

On June 8, 1949, a collection of 18 individuals of *S. texanus* was made from one of the pools, both of which contained fairy shrimp in large numbers. Both sexes were represented in this collection by mature individuals, the 7 males averaging 15 mm. in length and the 11 females averaging 16 mm. On June 22 the pools were revisited, an abundant population of anostracans were observed in both, and further collections were made. Both sexes were fully mature and ranged up to 19 mm. in length.

On July 6, 1949 and on July 27 both pools were observed to be completely dried up.

The rainy period of August 5–9, previously described, refilled the basins. When visited on August 10, one pool was seen to contain about twelve inches of water and the other about seven inches. Both pools harbored very large populations of small, immature *S. texanus* ranging from three to five mm. in length. Two days later, on August 12, the average size of the fairy shrimp had increased to about 9 mm. for both sexes.

The August 12 visit was made at about 3:00 P.M. on a hot day. Apparently the fairy shrimp were more numerous at the sunny end of the

partially shaded pool. With the air temperature (shade) at 34.2° C., the water temperature of the partially shaded pool was observed to be 34° C., and that of the shallower unshaded pool, 36.4° C. These are very high temperatures to be tolerated by anostracans, most of which are considered to be cool-water dwellers. However, the resistance to high temperatures of *S. texanus* is not unexpected in view of the nature of the habitats, the seasons of occurrence, and the region of the country in which the species is found.

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THE PLANT AND ANIMAL ENVIRONMENT: A FRONTIER

An ecologist, in the broadest sense of the word, must be an environment specialist. He must be not only a botanist or a zoologist, but he must be more than just familiar with the environment in which his plants and animals live. He must be meteorologist, soil physicist, geologist, and geographer, or he must ally himself with these specialists. Furthermore, if he has any hope of performing a synthesizing function, he must be physiologist and geneticist as well. In a professional sense, no man can be all of these. Rather, a man specializes in the things nearest and dearest to his heart, and he picks up what he considers necessary from the others as he goes along.

Scientists specialize more and more as they pursue their chosen fields, so that there are now autecologists, synecologists, animal geographers, plant sociologists, and the like. And there are synoptic meteorologists, micrometeorologists, climatologists, and so on in a related science. Synthesis becomes more and more difficult for the individual man, however broad his training and experience. An inevitable result of this over-specialization and attendant difficulty of synthesis is to miss the fundamental, albeit complex, relations of organisms to environment, and perhaps to reach invalid conclusions. Moreover, those portions of the sciences which are interrelated should be considered together. From this common consideration may come methods of attack on problems in one field which could be used in others. Since it appears that a life-time is fast becoming insufficient time for a man adequately to prepare for the synthesizing function, cooperation of the specialists and coordination of their subject matter are required. This is done on a limited scale, of course, when a botanist whose specialty is ecology approaches a soil physicist on a knotty problem involving, for example, the accurate measurement of soil moisture. Both scientists will probably need an instrument specialist or an electrical or electronic engineer to help solve the purely instrumental problem (Condon '49). And they will probably need the services of a statistician before they are through accumulating data.

What seems to be needed, in addition to conventional individual research, is a community of

scientists, working together, and discussing together aspects of the common problem on which they are working. They must write in each other's journals. Happily, this is occurring more often lately than ever before. Even the *Review of Scientific Instruments,* a publication of the American Physical Society, has a section on instrumentation for the biologist. Wiener ('48) has made a strong case for the scientific community in his new science of cybernetics, now a few years old.

There appears to be a good opportunity for this kind of cooperative endeavor where ecology is concerned. Animals affect the plant environment, just as the distribution of plants affects the distribution of animals: both live and have their being on the earth and in its atmosphere or in the water bodies of the earth; even an individual organism is in a sense a part of its own environment—a withered leaf reduces food production in the plant; an injured foot may mean death for the animal through infection, or helplessness before predators. Moreover, soil, air, and water compose the physical environment which affects and is affected by the organisms therein. It seems to me that an adequate ecological research program must number among its professional personnel not only botanists and zoologists, but meteorologists, geologists, geographers, oceanographers, mathematicians, soil physicists, biochemists, biophysicists, electrical engineers, and any other specialists needed in the solutions of the problems involved in the complex interrelationships of organisms and their environment. Even the archaeologist is providing assistance with regard to certain phases of the prehistoric environment in helping to uncover postglacial climatic cycles (Campbell and Krieger '49), a contribution of some moment, since climatic data more than a century old are rare indeed.

The most forward step in recent years is apparently the one represented by the opening of the Earhart Plant Research Laboratory at the California Institute of Technology. The scientists whose foresight and initiative are responsible for the creation of this environmental laboratory are to be congratulated, and it is sincerely hoped that many problems heretofore considered too complex will bow before the concerted attack of a community of scientists.

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BOOK REVIEWS

Recent Advances in Limnology

[Editorial Note. This is the first review of a series, planned as a continuing feature of Ecology. Leading students of various aspects of ecology will be asked to comment critically on important recent contributions to their respective fields, the choice of subjects for discussion to be made by the reviewers. They are expected not to confine their remarks to books bound in hard covers, or to works sent to Ecology by publishers. News notes about ecologists and their projects may be included. Unsolicited essays of this character by members of the Ecological Society of America and others will be welcomed by the Editors, who reserve the right to reject contributions regarded as unduly polemical, captious, propagandistic, or of insufficient interest to ecologists generally.]

The present review concerns itself entirely with some of the recent work done at the Institute of Freshwater Research, Drottningholm, Sweden, whose Report No. 29 has recently appeared.[1] It contains the Annual Report for 1948 by the Director, Sven Runnström, and twenty short papers. This is the first annual report to be published and contains a summary of the various phases of research in progress at the institute. Appended to it is a complete list of publications based on research done at the institute since its inception in 1932.

The majority of the papers are concerned with aspects of the ecology of the economically important freshwater fish of Sweden—trout, char, grayling, Coregonus, and eels. The two short papers on the bottom fauna of Swedish lakes represent but a small part of an extensive study of the bottom fauna. The results of this study are voluminous and merit separate treatment.[2] A preliminary report of a quantitative plankton study in Swedish lakes and a consideration of some problems of managing a crayfishery complete the list.

The substance of this review will be devoted to three papers, the contents of which can be treated under two headings, the coregonid problem and a consideration of selection for egg size and number in char.

The first subject is treated in a paper (**Svärdson, G.** The Coregonid problem. I. Some general aspects of the problem. pp. 89–101) concerned with some general aspects of the problem, as the title indicates, and is to be followed by more detailed reports. Svärdson has based his work on the hypothesis that geographical isolation is necessary before speciation can occur. Although this statement may appear unnecessary to many readers, it serves to emphasize a new approach to the problems of speciation presented by the coregonids. Other biologists of the present and the immediate past who have been concerned with this problem have accepted the possibility of ecological, non-geographic, isolation as an antecedent to speciation. Svärdson presents evidence that neither size at the onset of maturity nor any estimation of inherent "growth potential" have value as taxonomic criteria. Any genetic stock of coregonid can exhibit an astounding range of growth rates and sizes at maturity. This is easily demonstrated by transplantation to different lakes. The amount of food available to each fish is the only important environmental determinant of growth rate.

In many Swedish lakes several populations of *Coregonus* co-exist. Some are known from historical records to have maintained themselves for many years. These populations are considered separate species by Svärdson as indeed they must be. Differences in both time of spawning and type of spawning ground allow little, if any, hybridization. An illustrative situation was encountered in two adjoining lakes in north central Sweden. Four populations of *Coregonus* inhabit the Hornavan-Uddjaur lake system. "Asp," a comparatively large form, which probably spends the summer in the deeper layers of both lakes, spawns in streams at a depth of 0.5 to 1.5 meters during October. "Sellack," a smaller fish inhabiting both lakes, spawns in quiet waters, 3–5 m. deep, along the lake shore in January. "Storsik" spawns in quiet water 2–4 m. deep in mid-December. It occurs in both lakes. "Gråsellack," however, lives only in the deep waters of Lake Hornavan, the deeper of the two lakes. This population spawns at a depth of 100–130 meters. In this manner are the four populations reproductively isolated. The feeding habits of these four populations have not as yet been studied. Statistical analyses of meristic characters indicating the differences between the populations have been made and will be reported in subsequent papers of the series.

The existence of sympatric populations such as these, by requiring specific designation for each population, makes it immediately apparent that the assemblages hitherto considered to constitute the species *Coregonus albula* and *Coregonus lavaretus* are in reality groups of sibling species. *C. albula* and *lavaretus* therefore become superspecific designations. It is interesting to note that in the paper by Määr, cited

[1] **Institute of Freshwater Research, Drottningholm** (Fishery Board of Sweden). Rep. **29**, 152 pp. Annual report for the year 1948 and short papers. Lund, Carl Blom, 1949.

[2] See following review, "Chironomids of Swedish Lakes."

below, the chars of the Faxälven river system fall into five groups with different spawning times and types of spawning grounds. As populations of all five groups occur in at least one lake, it may be necessary to elevate each group to specific rank, making *Salmo alpinus* L. a superspecies.

Svärdson plans to place the taxonomic ranking of allopatric populations on a more sound footing by transplanting a sample of any population to be determined into a small lake with known stocks. There are a large number of possible interactions. The introduction of a third coregonid stock into a Lapland lake which had long supported two had the unexpected result of converting all three populations into a single panmictic, highly variable one. The characteristics of these stocks are unknown, but it is supposed that the former reproductive isolation of the original two stocks was destroyed by an overlapping of both spawning periods by that of the third.

The data illustrating geographical variation of egg size and number in the char (*Salmo alpinus* L.) come from the Faxälven River system of central Sweden (**Määr, A.** Fertility of char (*Salmo alpinus* L.) in the Faxälven water system, Sweden. pp. 57–70). This river system is well suited for such a study as there is a series of seven lakes along its upper course in which char live. All the lakes are oligotrophic, yet show a change in their characteristics as they are followed downstream. The egg samples were taken from ripe females on the spawning grounds. Only those fish which could not be stripped were used. The fish were weighed, the ovaries were removed and weighed, and the eggs were counted. The egg weight as a percentage of the weight of the female varied within the same limits in all populations. Total number of eggs per female varied considerably from lake to lake and to a lesser extent from population to population in the same lake. The largest egg numbers are found in the populations on the edges of the range of the char. The population with the highest egg number lives in Lake Leipikvattnet, a small (5 km.^{2}), headwater lake (altitude 468 m.). The next highest number, 55% of that characteristic of the Leipikvattnet population, is found in Lake Strömsvattudal, which is the largest lake in the system, with an area of 147 km.^{2}, and lies farthest down in the valley (285 m.). The populations of the other five lakes produced from 20 to 50% as many eggs as the highest value found. In these lakes the char are most numerous, apparently finding conditions optimal here. Char are least abundant in Leipikvattnet and Strömsvattudal and the fish tend to be larger.

The explanation advanced by Määr is more fully discussed in a review paper (**Svärdson, G.** Natural Selection and Egg Number in Fish. pp. 115–132.). In that part of its range where the species finds conditions optimal, char fry will be competing for food chiefly with other char fry. Studies of *Salmo trutta* fry (**Brown, M.** Journ. Exp. Biol. **22**: 118–129, 1946) have shown that large fry get more food and make faster growth than small fry. It is probable that large char fry have a similar advantage. Selection will then be strongly in favor of large eggs. As the weight of eggs which a char of a given size can produce is relatively constant, this increase in egg size will entail a decrease in their number. On the periphery of the range intra-specific competition is relatively unimportant and selection does not favor large eggs. Here, apparently, selection has found that there is safety in numbers.

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CHIRONOMIDS OF SWEDISH LAKES [1]

The most massive report yet to emerge from the remarkable Institute of Freshwater Research at Drottningholm, this is also the bulkiest volume yet published on lake bottom organisms. It is gratifying to discover that while it might have been somewhat shorter, its importance is roughly commensurate with its length. Handsomely printed and lavishly provided with tables and graphical illustrations, it is astonishingly easy to find one's way through, and is blessed with an index and a substantial summary in English. Its price in dollars is absurdly low that American workers, finding that the volume needs binding after a little use, will have to pay almost as much for a cloth binding as for the book.

The heart of the work is a thorough investigation of the quantity and composition of the bottom fauna of three lakes in the primary rocks of the south Swedish highland, carefully chosen to reveal the influence of increasing humus content on the bottom fauna of lakes

[1] **Brundin, Lars.** Chironomiden und andere Bodentiere der südschwedischen Urgebirgsseen. Ein Beitrag zur Kenntnis der bodenfaunistiechen Charakterzüge schwedischer oligotropher Seen. Institute of Freshwater Research, Drottningholm (Fishery Board of Sweden), Rep. 30, 915 pp., Lund, Carl Blom, 1949. Kr. 15.00.

that are rather similar in all respects but humus. All are regarded as oligotrophic, all are small and rather shallow, and only one, Skärshultsjön, a "moderately polyhumic" lake, is stably stratified in summer. The figures leave no doubt of the adverse effect of humus content: widening the series to include two other lakes almost equally well studied, it appears that as one goes from the extremely oligohumic Skären to the extremely polyhumic Grimsgöl, the profundal bottom fauna undergoes a six-fold decrease in numbers, from 1,900 to 300 organisms per square meter, or a five-fold decrease in weight, from 3.3 to 0.7 grams per square meter.

Changes in the littoral bottom fauna are roughly parallel to those in the profundal, although the great diversity of substrata in the littoral zone, both within and between lakes, makes comparisons more difficult. The fauna of the deepest bottoms actually increases in the polyhumic lakes, owing to the prevalence of *Corethra,* but the proportion of the total bottom area involved in this anomaly is probably negligible. It is a defect of the work that the proportions of bottom area at different depths are not stated or used in the calculation of averages, and a similar criticism can be levelled at the "averages" computed for the littoral zone. These averages are evidently not weighted for the varying proportions of total area occupied by the different substrata, though all the major plant associations (*Scirpus, Equisetum, Isoëtes, Nitella,* etc.) were studied intensively. In the absence of this essential information it is not possible to assess the benthic productivities of the lakes as wholes.

The data for the three (or five) best-known lakes in the Aneboda district are skilfully brought into a comparative setting by gradually extending the geographic area, first, to several other lakes in the same district that were studied at least once, then to the lakes of Växjö, which have been strongly eutrophied by sewage pollution, then to the province of Jämtland in north-central Sweden, where several lakes were previously studied by the author, and finally to lakes as far afield as the Alps, Germany, England, the Scandinavian Arctic, and Greenland. The comparisons are almost entirely qualitative, however, or if quantitative, they emphasize numbers of bottom organisms rather than weights. One reason for this is evidently that the weights given for the "home" district of Aneboda were obtained by averaging "weights of a comparatively large number of representatives of the animal groups in question" (translation of a footnote on page 420, the sole statement of a highly important methodologic question). Brundin presumably does not attach much significance to the results, nor would the reviewer, particularly without seeing the figures. It is not even stated explicitly whether the figures refer to "fresh" (formalin or alcohol) or dry weights, though it is obviously the former.

On the quantitative side, then, this study is workmanlike rather than imaginative, and while it is a great mine of some sorts of information about certain extremely interesting lakes, it suffers from glaring defects. All of this can be forgiven, however, when one realizes that the work belongs in another tradition altogether from that of modern quantitative ecology. In reality it is a stupendous piece of autecology, dealing with a group of animals, the Chironomidae, of a taxonomic difficulty unmatched in the animal kingdom. The taxonomic achievement is indicated by the casual statement that "practically all the chironomid larvae found in the lakes in Småland could be identified" (p. 857). It is documented by 140 pages discussing the geographic distribution and larval ecology of all the 300-odd species known from Sweden, and a further 40 pages of pure taxonomy, including the descriptions of two new genera and 15 new species. Rearing of larvae, the bugbear of limnologists concerned with this family, was accomplished not only in the laboratory but in the field, inverted funnel traps leading to submerged bottles half full of air having been placed over different types of bottom in several lakes. The value of this method for quantitative ecological studies, particularly of bottoms that cannot be sampled by dredging, has not been fully exploited by the author, but the new information about autecology of species, phenological information especially, is exceedingly important.

With a grip on the systematics of this key group that will be the envy of non-European limnologists for many years, Brundin embarks on a penetrating discussion of chironomids and lake typology. He makes short work, for example, of Lenz's "mesotrophic" *Stictochironomus* and *Sergentia* lakes, pointing out that the larvae in question, which came from Norway, belong to different species from those Lenz knew from central Europe, and have very different ecological significance. The conclusion, discouraging but inevitable, is that while chironomids may have some usefulness as indicators of the oxygen content of the bottom lake water, they are poor indicators of lake types in general; moreover, most of the literature of this subject is virtually worthless, as it is based on dubious generic rather than specific identification of larvae.

A single lake, Innaren, in the Aneboda district, has yielded 140 species of Chironomidae, or 70 per cent of the lacustrine species known from the whole district. It is a transparent oligotrophic lake, low in humus, and would be expected to have a diversified fauna, but even so the cold-stenothermal species are excluded by the high temperature of the hypo-

limnion. The most polyhumic lakes tend to have a restricted fauna of ecological specialists, and in general Brundin regards temperature as a more important factor than humus, or even oxygen content, in controlling the nature of the benthic chironomid fauna. In fact he calls for a return to the classical "biogeographic" concept of limnological zoology exemplified by the work of Zschokke, but while it is helpful and refreshing to have it pointed out that the profundal bottom fauna of central European lakes consists in large part of glacial relicts, even among chironomids, discussions of which environmental factors are more "important" for whole taxonomic groups seem rather pointless today. A single factor is hardly likely to be of equal importance for all members of a fauna consisting of 140 species .

The more reflective, comparative parts of Brundin's volume, including the discussion of lake typology, are colored by this rather old-fashioned, doctrinaire viewpoint, according to which it seems necessary to decide whether a given species is more sensitive to the "oxygen standard," the "nutrient standard," or some other, even more loosely defined suite of variables. In the total absence of observational data on the chemical composition of the bottom deposits, the oxidation-reduction potential of the micro-habitat in which the larvae are actually living, the nature and quantity of food required by a chironomid larva, or the real productivity of the lakes in question, critical ecologists are not likely to take these parts of Brundin's monograph very seriously. What they cannot afford to neglect is the huge amount of superb taxonomy and fine-scale autecology of a group hitherto regarded as unimaginably perplexing.

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The Evolution of "Climate through the Ages" [1]

Since its first appearance in 1926 this work has been part of the intellectual equipment of a whole generation of Earth scientists and paleoecologists. Its return in a new dress will occasion some mixed emotions on the part of its older admirers, at least one of whom has an affection for it that can only be compared with his parents' regard for Maude Adams. As one who made Miss Adams' acquaintance long after "Peter Pan," the reviewer will attempt to report honestly to a younger generation on Brooks' return engagement, but a clear-sighted account is probably not to be expected.

If this was a great book in 1926, it must be a great book today, for it has changed very little. The first part, dealing with principles, i.e., with the nature of climatic factors and their variation, remains, as it was when it was first written, a masterly exposition of general climatology. It is hard enough to prepare an orderly analysis of the climatology of a stable Earth, as many a forgotten textbook shows; to Brooks belongs the immense credit of re-thinking all his first principles in keeping with the shifting scenes of paleogeography, an incomparably more difficult task. The fundamental conclusion appears now to be generally accepted: that the "normal" climate of the geologic past was nonglacial, and that a concatenation of changes of small magnitude, of which an increase in average elevation of the land was most important, sufficed to bring about the profoundly "abnormal" climate of glacial ages.

Part II treats of the climates of the past, specifically of the peculiar climates of the Upper Carboniferous and the Pleistocene. Its greatest *tour-de-force* is the demonstration that the hypothesis of continental drift is not only unnecessary but insufficient to explain low-latitude glaciation during the latter part of the Paleozoic. This argument, to the reviewer, is as convincing as ever, given the paleogeography that Brooks accepts. Unfortunately our ideas of paleogeography change almost as radically as did the configuration of the continents during geologic time, and much more rapidly. In other parts of the new edition Brooks has shown little taste for doing the bulk of his library work over again, and one can only hope that no drastic revision of the Upper Carboniferous map of the world is required by recent research. The chapter on Pleistocene climates has been entirely rewritten, but it leans rather heavily on the fallible summary of Zeuner, and it is clear that Brooks has made no real attempt to come to grips with the enormous recent literature of this subject.

Part III, concerned with postglacial and historic climates, has been most thoroughly revised, but because the result is merely adequate, where much more might have been expected, it must be pronounced unsatisfactory. There is much to praise here, much of great interest, and little that is seriously wrong; the most important recent evidence has been seen and commented upon. But the most interesting information was already in the first edition, and

[1] **Brooks, C. E. P.** Climate through the ages. A study of the climatic factors and their variations. Revised edition. New York and Toronto, McGraw-Hill Book Co., 1949, 395 pp., $4.50.

the additions are curiously eclectic, as though only the minimum amount of work had been done to revise the part of the book that most needed revision. Thus the account of Kharga is brought more or less up to date, while nothing is said about the Faiyum; Schostakowitsch's annually laminated lake deposits are discussed, but Welten's are ignored; Nilsson's alleged lake terraces in the Nakuru-Naivasha basin are mentioned quite uncritically; the discussion of Lake Lahontan has a strangely antiquated flavor. Most surprising, perhaps, is the retention, in the new edition, of Huntington's path-breaking but thoroughly discredited hypothesis of climate and culture in the Maya country.

It will be evident from these remarks that "Climate through the Ages" is not a poor book, but a somewhat timeworn masterpiece. It remains much the same as it was, and if times have caught up with it, the book can take much of the credit and should not receive all the blame. The core of its argument, so far as the reviewer can see, is destined to endure, and it is extremely useful to have it re-affirmed at a time when a flood of new evidence bears witness to its soundness. The revision as a whole is not overly successful, but fortunately the parts of the work that stood in greatest need of revision are not essential to its reputation. It deserved better treatment than its author has been willing to give it in the new edition, but not all revised editions can be so satisfactory as those of Linnaeus. Probably nothing better shows the influence of "Climate through the Ages" than the realization that a proper revision would require the integrated efforts of a corps of experts. Each would be capable of emending minutiae, but the main point is that all would have been nourished in the grand tradition of the book itself.

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The Vegetation of the Great Rift Valley [1]

One of the most remarkable products of Belgian rule in the Congo is the system of national parks established by beloved King Albert I. The most interesting of these is the Parc National Albert, which lies in the Great Rift valley in the basin of Lake Edward across the border from Uganda and is designed to protect the mountain gorilla and the forests which it inhabits. Included within the Park are the Virunga volcanoes (elev. 3,056–4,507 m.) to the south and the vast massif of Ruwenzori (elev. 5,119 m.) to the north, past which the lake drains through the Simliki River to Lake Albert and thence to the White Nile. The area must be the most complex biogeographically in Africa, for in addition to its diversified physiography it is on the western border of Engler's East African province and is sufficiently close to all the other four provinces to partake to some extent of their floristic elements.

The greater area of the Park consists of the lacustrine alluvia of Lake Edward (surface elev. 916 m.) together with those of Lake Albert to the extreme north. In the extreme south the Virunga volcanoes are surrounded by a lava plain, in some places of recent origin. The mountainous western escarpment of the Rift is formed chiefly of shists and quartzites and their derivatives. The massif of Ruwenzori consists of precambrian crystalline rocks, the higher summits covered with permanent glaciers above the altitude of 4,450 m., with tongues descending to about 4,200 m. Traces of past glaciation are evident to about 3,330 m.

The bioclimate of the Parc National Albert is composed of an interplay of temperature, precipitation, and prevailing winds. Since the area is one of sharp relief, temperature varies accordingly; in general there is a diminution of 0.5° C. per ascent of 100 m. elevation. At Rwindi, situated on the gently sloping plain south of Lake Edward, the mean annual temperature is 23.6° C. with a daily range of about 14° C. At an altitude of 4,200 m. upon Ruwenzori the annual mean is 2° C. with a daily range of −2° to 6° C.

Precipitation in the basin of Lake Edward varies annually from 850 to 1,200 mm. and consists of convexional downpours. There are the usual two equatorial rainy seasons, one from the beginning of March until the middle of June and the second from mid-September to mid-December, interrupted by two dry seasons corresponding to the solstices. Evaporation is intense. Precipitation in the mountains is somewhat stratified, increasing from the plains to a maximum of 2,250–2,400 mm. between 2,200 and 2,500 m. elevation and thence decreasing sensibly but variably: at the summit of Karisimbi Volcano (4,507 m.) the annual mean is 943 mm.—about equal to that at the level of the lake. On Ruwenzori, however, the maximum near 2,200 m. elevation is about 4,000 mm. annually, falling at the summit to about 1,600 mm.

[1] **Walter Robyns.** Flore des Spermatophytes du Parc National Albert. Institut des Parcs Nationaux du Congo Belge, Bruxelles. Vol. I, pp. lvi + 743, colored frontisp., 2 maps, 33 photogrs., 86 pls., bibliogr., ind., 1948; Vol. II, pp. 626, 1 map, 32 photogrs., 54 pls., bibliogr., ind., 1946. 11 × 7 inches; each vol. 750 fr. Belg. ($15 U. S. A.).

Air currents, of course, have much to do with the pattern of precipitation, and these are particularly important since the graben of central Africa is the center of convergence of three prevailing winds: from the South Atlantic, from the southern Indian Ocean, and that from the northeast, blowing the whole length of the Rift from the valley of the Nile. The last, with the foehn from the higher mountains, is the chief desiccating agent, and together they would seem to account for the altitudinal maxima of precipitation mentioned previously.

Elevation, temperature, prevailing winds, and precipitation mold the plant formations of the Park. The basin of Lake Edward is occupied by a savanna vegetation dominated by *Themeda* and *Heteropogon,* together with such other grasses as *Hyparrhenia.* In greater part, the basin savanna is interspersed with thickets of spiny acacias (especially *A. hebecladoides*) and *Borassus aethiopium.* South of the lake, the plain of the Rutshuru River is distinguished by the development of associations of such succulents as *Cyanotis, Rhynchelytrum, Aloe, Sanseviera,* and *Kalanchoe.* This formation, in turn, is transitional to that of the Virunga lava plains extending southward to Lake Kivu (elev. 1,460 m.). Some of these lavas date as recently as 1912, and Professor Robyns has studied the succession of colonization from the first lichens (*Stereocaulon*) and various mosses, to ferns (*Pteris vittata, Polypodium,* etc.), to succulent annuals, and finally to discontinuous thickets of *Myrica salicifolium, Erythrina abyssinica,* etc.

At the extreme north of the Park, in the valley of the middle Simliki River, a tongue of the Congo lowland rainforest crosses the Rift, extending to Lake Victoria in Uganda. The forest is almost homogeneous *Cynometra Alexandri* in the Park, but includes various species of such genera as *Celtis, Ficus, Strombosia,* and *Erythrina,* together with many lianes; it reaches to about 1,750 m. upon the slopes of Ruwenzori.

The montane formations assume much the same stratification whether upon the massif of Ruwenzori, the Virunga volcanoes, or the dorsals of the graben, altitude permitting. These vegetational strata are, in order, the mountain rainforest, the bamboo forest, the forest-prairie of arborescent heaths, and the alpine formations. The mountain rainforest extends roughly between 1,750 and 2,500 m. elevation and coincides with the belt of maximum precipitation. It is distinguished easily from the lowland rainforest through the relative absence of lianes, although epiphytes are more abundant. Conspicuous tree genera include *Podocarpus, Hagenia,* and *Pygeum.*

Between elevations of 2,300 and 2,600 m. an interesting formation is the bamboo forest, which in this case is composed of dense stands of *Arundinaria alpina* with culms attaining 20 to 25 m. in height and 18 to 20 cm. in diameter at the base. Openings in the bamboo are occupied by such herbaceous genera as *Clematis, Viola, Sanicula.* On the higher Virunga volcanoes a special formation is intercalated above the bamboo, namely, a forest-prairie or alpine woodland of *Hagenia abyssinica,* a stout but rather low tree of Rosaceae which is interspersed amongst giant herbs belonging to such genera as *Rumex, Geranium, Stachys, Vernonia,* and particularly two umbellifers: *Chaerefolium sylvestre* and *Peucedanum Kerstenii.*

Directly above the bamboo forest, or the *Hagenia* forest-prairie as the case may be, is found the arborescent heath formation, so characteristic of highland tropical Africa, between elevations of roughly 2,600 and 3,600 m. Here the woody plants consist largely of *Erica arborea* and *Phillipsia Johnstonii,* festooned with filamentous lichens such as *Usnea* and other epiphytes. In openings populated by sub-shrubby Hypericums, Senecios, and Lobelias, are bogs of *Sphagnum planifolium.* Above 3,600 m. elevation is the alpine formation with its obelesque-like arborescent Senecios and Lobelias and its alpine pastures of *Alchemilla.* All in all, the picture which Professor Robyns paints recalls to the reviewer nostalgic memories of the montane flora of Central America, with vicarious species, genera, or even families, of course (*Chusquea* instead of *Arundinaria; Thibaudieae* instead of *Ericeae; Puya* instead of the tree Senecios and Lobeliads), where analogous formations have much the same altitudinal limits. At about 4,300 m., which is to say at about the lower limit of the glaciers upon Ruwenzori, the vegetation finally is reduced to certain mosses and mats of the lichen *Umbilicaria* on the exposed rock and talus.

"Flore des Spermatophytes du Parc National Albert" is the most ambitious general study published to date upon the most varied and interesting vegetation of Africa. It represents many years of painstaking preparation by botanists working both in Brussels and in the Congo under the inspired leadership of Professor Robyns and his great predecessors, Th. Durand and E. de Wildemann. Although the greater bulk of both volumes consists of systematics (including analytical keys, somewhat abbreviated descriptions, but quite detailed bibliographies, citations of exsiccatae and distributional data), the easily read introductory chapters alone should be of keen interest to all who are concerned with the natural history of tropical Africa. The text is liberally interspersed with maps and photographs and many superbly detailed, full page drawings.

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Charles Darwin [1]

This is a remarkable and in many respects inspiring analysis of the reasons for Charles Darwin's potent influence on modern thought. Due to the conditions prescribed by the publishers of the Twentieth Century Library, the book is not so much an account of the life and work of the great evolutionist as an appraisal of his influence on the intellectual currents of modern times. Paul Sears has been extraordinarily successful in fulfilling the purposes of this series in that he has approached his subject with breadth and understanding and with a high degree of perspective.

The book is especially important at this very time because of the following circumstances. It will be recalled that for about 150 years prior to the beginning of this century an intellectual movement occurred which in many respects was one of the most revolutionary in all human history. This movement resulted in the creation of an immense structure of knowledge, in effect, the establishment of the biological sciences. The names of remarkable leaders in thought during this period readily come to mind —such men as Linnaeus, Buffon, Lamarck, Goethe, Treviranus, Haeckel, Erasmus Darwin, Thomas Henry Huxley, and a number of others. The movement may be said to have culminated in the pronouncement of Charles Darwin's theory of evolution. The impact of this upon men's minds was greater than that of any pronouncement which one can recall. Several decades were to pass before its general acceptance. In effect, the Darwinian Theory proved that man was an integral part of nature itself, and not a separate and independent being.

It became evident soon after the commencement of the present century, however, that powerful counterforces were being brought into play. They have gone far towards blinding man's eyes to his essential dependence upon nature. Within the last fifty years this other revolutionary burst in man's intellectual development has profoundly affected present-day philosophy and our general outlook on life. The cause can be attributed to the extraordinary advances that have been made in the mathematical and physical sciences. As we well know, the growth of these sciences has, among other things, resulted in the development of innumerable inventions which have enabled man to master the air, to use radar, and even atomic power. As a result, we are apt to be tricked into believing that we are "the masters of the universe" and to overlook, if not forget, our essentiality and oneness with the natural world.

In writing this book, Paul Sears has drawn upon his extensive knowledge of thinkers and philosophers including those who have been dedicated to fields of interest other than the biological sciences. In effect, this is a luminous story of the development of human thought woven around the life and work of the great evolutionist, enriched by the author's own rare gifts of perception and wisdom.

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New York, New York

[1] **Sears, Paul B.** Charles Darwin, The naturalist as cultural force. New York: Charles Scribner's Sons, ix + 124 pp., 1950. $2.00.

ERRATUM

In the paper by Lull and Ellison, "Precipitation in relation to altitude in Central Utah," published in Ecology, Vol. 31, *Picea glauca* (line 1, p. 480) should read *Picea pungens*.

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